ARTICLE IX.

THE MAMMALIA OF THE UINTA FORMATION.

PART I. THE GEOLOGICAL AND FAUNAL RELATIONS OF THE UINTA FORMATION.
PART II. THE CREODONTA, RODENTIA AND ARTIODACTYLA.

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PART III. THE PERISSODACTYLA.
PART IV. THE EVOLUTION OF THE UNGULATE FOOT.

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ILLUSTRATED BY FIVE LITHOGRAPHIC PLATES AND THIRTEEN DIAGRAMS.

Read before the American Philosophical Society, May 17, 1889.

This memoir is principally descriptive of a collection made by the Princeton Scientific Expedition of 1886 in the Bad Lands of the White River, Northeastern Utah. The party was composed of Messrs. Reynolds, Harlan, Hervey, Baucus, Paton, Kane, all Princeton students, under the able leadership of Mr. Francis Speir, Jr., whose name is connected with so many important palæontological discoveries. The expedition experienced great difficulties in the field and some risk from the hostile threats of the White River Utes.

The collection has been skillfully prepared and mounted by Dr. Franklin C. Hill. The drawings are by Mr. Rudolph Weber.

PART I.

BY WILLIAM B. SCOTT

GEOLOGICAL AND FAUNAL RELATIONS OF THE UINTA FORMATION.

While the palæontological relations of the various series of Eocene deposits in the upper Green River valley are, for the most part, quite clear, the stratigraphical relations are as yet but imperfectly known, and leave many questions still open. Dr. White (No. 18, p. 35) believes that the entire series is conformably deposited: "In the great region now drained by the Green river, there are three well-marked groups of strata, that come in their order above the Laramie group, and which all agree in referring to the Tertiary period. These are the Wasatch, Green River and Bridger groups, named in ascending order. The Wasatch group is the lowest of a series of three fresh-water Tertiary groups, all of which are intimately connected, not only by an evident continuity of sedimentation throughout, but also by the passage of a portion of the molluscan species from one group up into the next above. Not only were the three groups, aggregating more than a mile in thickness, evidently produced by a continuous sedimentation, but it seems equally evident that it was likewise uninterrupted between the Laramie and Wasatch epochs, although there was then a change from brackish to fresh waters and a consequent change of all the species of invertebrates inhabiting these waters."

King, on the other hand (No. 6, p. 353 *et seq.*), adduces evidence to show, not only that the Wasatch and Laramie are very clearly separated by unconformities, but that the three Eocene series are likewise divided by lack of conformity with each other.

Palæontologically the arrangement of the series is less obscure, though if we accept White's view of a continuous sedimentation from the Laramie to the Bridger we shall meet with very formidable difficulties. Thus no place is left for the very peculiar and primitive fauna of the Puerco group, which is not at all represented in the northern basin; the same reasoning will apply to the transition fauna of the Wind River group, a formation estimated as being 1000 feet or more in thickness (St. John, No. 12, p. 260), but so far as is yet known confined to the Wind River valley. To assume that the Puerco is contemporaneous with the Wasatch, the Wind River with the Bridger, and the beds of the Bridger basin with those of the Washakie

basin, would involve very complicated hypotheses of barriers and migrations for which there is no present evidence. The fauna of the Wind River deposits has been shown by Cope (No. 1) to be intermediate between the Wasatch and the Bridger, mingling types which elsewhere are found only in one or other of these formations with some forms peculiar to itself. Thus such typically Wasatch genera as *Coryphodon*, *Phenacodus*, *Didymictis*, *Calamodon* and *Esthonyx* are associated with equally typical Bridger genera, *Palæosyops*, *Lambdotherium*, *Miacis* and *Microsyops*, while the earliest and smallest known member of the Dinocerata, *Bathyopsis*, is confined to these deposits. Thus the Wind River formation occupies the same intermediate position between the Wasatch and Bridger palæontologically as does the Green River stratigraphically. One is therefore led to infer with Cope (No. 2, p. 453) that the Green River and Wind River are parts of the same formation, though the entire absence of mammalian fossils from the former renders this determination somewhat uncertain. It may perhaps be objected to this view that in Southwestern Wyoming the Bridger beds lie conformably upon the Wasatch. This conformity is, however, not improbably deceptive, for the following reasons: (1) King states (No. 6, p. 380) that he has observed unconformities between the Wasatch and Green River beds. "In the region east of the Wasatch a large amount of the Vermilion Creek [Wasatch] series was left in a nearly horizontal position and the sediments there sank quietly through deep water upon an approximately level bottom, accumulating in strata nearly conformable with the underlying Vermilion Creek rocks. From the manner in which the rocks of the Green River group abut westward against the Vermilion beds, it is evident that there was in the region included between the Wasatch and Uinta a highland lifted above the lake of the Green River period." (2) The direct contact between the Wasatch and Bridger strata at the west of the Bridger basin takes place by the latter bed's *overlapping* the Green River and thus reaching the Wasatch. If we assume that the Green River shales represent a distinct series, this overlap can be explained only by supposing either that these beds had been swept away from the western part of the basin before the deposition of the Bridger series, or, what is much more probable, that a series of disturbances first contracted and then expanded the waters of the lake. (3) It is impossible to account for the faunal differences between the Wind River and the Wasatch on the one hand and the Bridger on the other on geographical grounds alone, as this area is encompassed both on the north and the south by typical Wasatch beds.

The balance of evidence would thus seem to point to the conclusion that the Wind River beds are to be regarded as forming the base of the Bridger series, and this view has the further advantage, that the Bridger, thus defined, is characterized

throughout by the presence of some form or other of the Dinocerata, and that this extraordinary group of animals is entirely confined to this formation.

A still more intricate and difficult problem is that with reference to the relations of the various areas of Bridger deposits (apart from the Wind River series) to each other. Of these areas there are three: (1) The Bridger basin west of the Green river; (2) the Washakie basin east of the same river, and (3) a small area to the south-east of the latter. Supposing the Bridger beds of the Washakie and Bridger basins to have been deposited conformably in the same lake which laid down the Green River series and to have been uplifted together with the Green River in a post-Bridger upheaval, it is not a little remarkable that erosion should have removed the Bridger from all parts save the middle of these two basins. The few observations which bear upon this point in the way of the dips of the two formations combine to indicate that the movement took place at the end of the Green River period, that the western lake [i. e., the supposed extension of the Green River lake west of the Wasatch mountains] was extinguished by this upheaval, and that the waters of the period formed a lake of restricted area altogether within the basin of Green river. Even with this supposition, which I conclude to be the most probable until it may be varied by future evidence, there is left the shadow of a doubt, whether the three Bridger bodies which appear upon our map—that of the Bridger basin, the Washakie basin, and the region east of Vermilion creek—were parts of a continuous sheet, or whether they themselves were areas of special lakes in the same general basin, but characterized by great fauna resemblances." (King, No. 6, p. 396.)

The facts of stratigraphy, so far as at present known, leave this question an open one, but the assemblage of fossils seems to point to the conclusion that there were at least two distinct lakes, and these not contemporaneous, but successive, a conclusion which we have already indicated elsewhere (Osborn, No. 10, p. 13; Scott, No. 15). The faunal lists of the two basins seem to show that the Bridger contains slightly older deposits than the Washakie, though the two may be in part contemporaneous. Some of the differences to be noted are, no doubt, due in part to the fact that the Bridger basin has been much more frequently and thoroughly explored than the Washakie, and others probably to conditions of preservation, for within the limits of the Bridger basin there are localities and strata which are especially rich in certain sorts of mammals which elsewhere are much rarer. As an example of this may be mentioned the abundance of the lemuroids and other small mammals at Twin Buttes. Future explorations may perhaps therefore diminish the number of faunal differences between the two areas.

A striking fact is the greater richness and variety of the forms found in the

western basin, especially of the smaller mammals, the creodonts, lemuroids and insec-
tivores, which are comparatively rare in the Washakie and very abundant in the
Bridger. No tillodonts have yet been reported from the former. The perissodac-
tyls are quite different. *Palæosyops* is somewhat less abundant in individuals in the
eastern basin, but *P. major* and *paludosus* are both present, and there are in the
Princeton Museum two undescribed species of this genus from the Washakie which
differ markedly from any yet found in the Bridger, and one of them, by its great size,
seems to approximate closely *Diplacodon*. *Hyrachyus* is represented by the same or
similar species and in about equal numbers in both areas. On the other hand the
Uinta rhinoceros *Amynodon* (= *Orthocynodon* nobis) is found only in the eastern
region, and the same is almost certainly true of *Triplopus*, while *Colonoceras* occurs
only in the Bridger basin. Among the artiodactyls the chief difference is to be
found in the presence and frequency in the eastern basin of the large species of
Achænodon, *A. insolens* and *A. robustus*. *Helohyus* and *Homacodon* have not yet
been reported from this region, but as representatives of these series occur in the
Uinta, we may confidently expect that they will be found in the Washakie.

Another striking difference between the two basins is to be found in the *facies*
of the Dinocerata so common everywhere. The great variability of these animals
precludes the making of any very sharp distinctions between those of the two areas,
but in a general way and with some exceptions they are in rather strong contrast
with each other. The prevailing type of skull in the Bridger basin is comparatively
short and broad, the nasal tuberosities are of moderate size, the parietal protuberances
are placed well forward, and the parieto-occipital crest is of moderate height. The
Washakie forms have generally a long narrow skull, with very large nasal tuberosi-
ties, the parietal protuberances are placed far back, the parieto-occipital crest is very
high; the cervical vertebræ in these species are also as a rule shorter than in those
of the Bridger area, and the animals tend to become of a larger size.

Making all due allowance for sources of error, it is difficult to believe that these
differences are to be explained by geographical considerations, while on the other
hand the stratigraphical relations of the Washakie beds to the underlying Green
River series present objections to the assumption that the latter could have been a
land surface for any great length of time. But these relations are by no means clear
and very much need to be re-examined.

We have no information relative to the small area east of Vermilion creek, but
in all probability it is simply an outlier of the Washakie.

From present knowledge, we are therefore justified in making a threefold sub-
division of the Bridger epoch, with the Wind River beds at the base and the

Washakie at the top, and in regarding the Dinocerata as the group characteristic of the entire epoch. It is interesting to note that where the fauna of the Washakie basin departs from that of the Bridger basin, it does so in the way of resemblance to the Uinta.

The geology of the Uinta formation is even more imperfectly known than that of the earlier formations. Dr. White says of it (No. 18, p. 37): "Resting directly, but by unconformity of sequence, upon all the Tertiary or Cretaceous groups in the region surrounding the eastern end of the Uinta Mountain range, is another Tertiary group that has received the name of 'Uinta Group' from Mr. King, and 'Brown's Park Group' from Prof. Powell. It is possible that this group was deposited continuously, at least in part, with the Bridger group, but at the places where the junction between the two groups has been seen in this region, there is an evident unconformity, both by displacement and erosion." Dr. White has also informed us (orally) that the mollusca of these beds are strikingly different from those of the earlier Eocene. The Uinta deposits are composed of sandstones and clays much like those of the Bridger in appearance. They are of no great thickness and are best developed in the valley of the White River, a tributary of the Green, in eastern Utah and Western Colorado. The mammalian fauna of the Uinta formation, while very distinctly of more modern character than that of the Bridger, is nevertheless quite closely allied with it, more especially with that of the Washakie subdivision, and it should be further remembered that this fauna has as yet been only very partially explored, and we may therefore expect that future discoveries will fill up many of the gaps still existing.

The more extended study of this fauna confirms the generally accepted view that the Uinta group should be placed at the summit of the Eocene, forming the transition to the White River Miocene, with which it has many affinities. The most striking and obvious difference from the Bridger fauna consists in the absence of the great Dinocerata so characteristic of this series, of which no trace has yet been found, nor is it likely that they will be discovered in the future. If present at all, this group must have formed but a rare and unimportant factor in the assemblage of Uinta mammals. Another Bridger type of which no member has been discovered in the Uinta (with a possible exception hereafter to be mentioned) is that of the Tillodontia, which seem to have finally disappeared, unless, as some have supposed, we are to look for their successors in the Edentata. The smaller mammals are very much more scantily represented than in the Bridger, though some of this difference is perhaps due to conditions of preservation, as indeed the Uinta fossils are scantier and less well preserved than in the immediately preceding or succeeding epochs. A simi-

lar, though less striking, difference exists between the Bridger and Washakie basins with regard to the number and variety of the smaller forms. The great assemblage of lemuroids and pseudo-lemuroids which the Wasatch and Bridger show so abundantly is thus far represented in the Uinta only by the single species *Hyopsodus gracilis* Marsh; the Insectivora, Chiroptera, and Marsupialia have not been found at all, though there is hardly room for doubt that they existed, inasmuch as they occur both in the Bridger and the White River. Rodentia are also rare and only one form can be certainly named, a species of *Plesiarctomys*, which genus is abundant in the Wasatch, Wind River, and Bridger beds. A second species of rodent is apparently implied by a lower incisor with a fragment of the mandible; it is, however, much larger than any known rodent of the Bridger or White River, and may possibly belong to some tillodont; but this is not at all probable, as the tooth is much more like that of a rodent, besides being smaller than that of any Bridger tillodont. We have still therefore to search for the forerunners of the beavers, mice, and hares of the White River.

So far but a single creodont is certainly known to occur in the Uinta fauna, a very large species of *Mesonyx*. This family ranges therefore throughout the Eocene of North America, being represented by *Dissacus* in the Puerco, *Pachyœna* in the Wasatch and *Mesonyx* in the Bridger and Uinta. The absence of the upper molars from the specimen before us precludes the possibility of a final reference of it to *Mesonyx*; but there can be no doubt that it is a member of the family. A second creodont is perhaps indicated by a small lower sectorial molar and a premolar; if so, the animal must have belonged to the *Miacidœ*, or it may be a true carnivore. The creodont nature of the specimen is the more probable on account of the greater likeness of the Uinta fauna to the Bridger. In any case this animal very probably represents the forerunner of the dog-like forms of the White River, the so-called *Amphicyon* and *Galecynus*, and possibly of *Dinictis* as well. Nothing is as yet known of any Uinta forms which would serve to connect the hyænodonts of the White River with the *Oxyœna* and *Protopsalis* of the Bridger.

The Perissodactyla of the Uinta are of great interest, as they are plainly intermediate between those of the Bridger and those of the White River. The curious family of *Titanotheridœ* has its Uinta member in *Diplacodon*, which thus connects the Bridger genera *Palœosyops* and *Leurocephalus* with the *Titanotherium* (*Menodus*) of the White River. *Hyrachyus*, so frequent in the Bridger, has apparently disappeared, its place being taken by *Triplopus*, which already occurs in the Washakie beds, though sparsely. In the Uinta it is one of the most abundant of all the fossils, and is highly characteristic of the formation. Another genus, rare in the Washakie,

abundant in the Uinta, is the rhinoceros-like *Amynodon,* a hornless form which is followed in the White River by *Metamynodon* and *Aceratherium.* The Uinta tapir is *Iscotolophus,* which is as yet represented by a single abundant species of small size. This genus appears to be represented also in the Bridger, at least there is a well-preserved specimen in the Princeton Museum which we cannot distinguish from it, and seems to have its representative in the White River beds, which Dr. Leidy has doubtfully referred to *Lophiodon,* though only for the reason that the specimen, an isolated last lower molar, could not well be distinguished from the corresponding tooth of that genus. As Leidy has suggested, this specimen most probably belongs to a very different genus (No. 7, p. 239). The equine series is represented in the Uinta fauna by two species of *Orotherium (Epihippus)* which stands just intermediate between *Pliolophus (Orohippus)* of the Bridger and *Mesohippus* of the White River, though it also is found in the Bridger.

Perhaps the most striking change in the facies of the Uinta fauna as compared with that of the Bridger lies in the importance suddenly assumed by the selenodont artiodactyls. The Bridger is not known to contain any forms which can be strictly called selenodonts, though *Homacodon* and *Helohyus* are obviously commencing to develop this type of dentition. The Uinta contains at least two clearly marked genera of selenodonts, if not more, which are very rich in individuals and thus give a very different aspect to the fauna as a whole. Of these the most abundant is *Protoreodon,* the unmistakable ancestor of the *Oreodontidæ,* the peculiar family which is so eminently characteristic of the American Miocene. By the five-lobed construction of the upper true molars, *Protoreodon* indicates the line of connection with the bunoselenodonts of the earlier Eocene, especially, if we may judge from the molar teeth alone, with *Helohyus.* The other clearly defined Uinta selenodont is *Leptotragulus,* the most ancient unequivocal member of the Tylopoda and closely related to the White River genus *Poebrotherium,* though in many respects more primitive. The absence of the upper molars from our specimens prevents comparison of this type with *Homacodon,* from which it was perhaps derived. The Uinta has thus yielded forerunners of the two most important and characteristic groups of White River selenodonts; it remains for future investigation to bring to light the ancestors of *Leptomeryx* and *Hyopotamus,* though the latter is not improbably an immigrant from the Old World. No Bunodonta have as yet been found, and the origin of the White River genera, *Perchoerus, Entelodon,* etc., is still obscure. Our knowledge of the Bridger bunodonts is still very imperfect.

It will be evident from the above statements that the affinities of the Uinta fauna are most closely with the Bridger, as at least five genera are common to the

two horizons, *Plesiarctomys, Mesonyx, Triplopus, Amynodon* and *Orotherium*, while on the other hand no genus passes through from the Uinta into the White River, unless one agrees with Cope (No. 2, p. 455) in regarding *Metamynodon* as identical with *Amynodon*. While this is true, the Uinta fauna is no less clearly the forerunner of the White River fauna; what there are strong reasons for believing to be the ancestors of the hyracodonts, the titanotheria, the rhinoceroses, horses, tapirs, camels and creodonts, the dog-like carnivores, and the sciuromorph rodents of the White River, all are to be found. We cannot therefore agree with Schlosser (No. 13, p. 60) in regarding this formation as Oligocene, which in fact seems to be an unnecessary term in the classification of our Tertiary lacustrine deposits, the division between the uppermost Eocene, represented by the Uinta, and the lowermost Miocene, represented by the White River, being quite sufficiently clear.

The following partial list of genera will indicate the relations between these three formations. The Wasatch genera, which penetrate only into the Wind River beds, are omitted from the list:

BRIDGER.	UINTA.	WHITE RIVER.
Dinocerata		
Tillodontia		
Stypolophus		
Mesonyx	Mesonyx	
Miacis	? Miacis	
Oxyæna	?	Hyænodon
Protopsalis		
		Daphænus (Amphicyon)
		Cynodictis
		Dinictis
		Hoplophoneus
Antiacodon		
Anisacodon		
Passalacodon		
		Leptictis
Ictops	?	Ictops
Plesiarctomys	Plesiarctomys	Sciurus
		Gymnoptychus
		Heliscomys
		Ischyromys
Colonymys		Eumys
Mysops		Palæocastor
		Palæolagus
Omomys		
Hyopsodus	Hyopsodus	Laopithecus
Tomitherium	?	Menotherium
Limnotherium		
Microsyops		
Xiphacodon		Didelphys
Helohyus	Protoreodon	Oreodon
	?	Agriochœrus
Homacodon	Leptotragulus	Poebrotherium
Achænodon	?	Entelodon
		Perchœrus
		Leptochœrus
		Hyopotamus
		Leptomeryx
		Hypisodus
Lambdotherium		

BRIDGER	UINTA.	WHITE RIVER.
Palæosyops		
Telmatotherium	Diplacodon	Titanotherium
Isectolophus	Isectolophus	Mesotapirus
Hyrachyus		
? Triplopus	Triplopus	Hyracodon
Orotherium	Orotherium	
Pliolophus		Mesohippus
Colonoceras		
Amynodon	Amynodon	Metamynodon
		Aceratherium
Nyctilestes		Domnina
Vesperugo		
Nyctitherium		

PART II.

BY WILLIAM B. SCOTT.

THE CREODONTA, RODENTIA, AND ARTIODACTYLA.

PRIMATES.

HYOPSODUS GRACILIS Marsh.

This species is the only one of the pseudo-lemuroids which has as yet been reported from the Uinta deposits. This group is exceedingly abundant in the Bridger, especially in the Bridger basin; it has become more rare in the Washakie, and although the Uinta has yielded but one species as yet, others will no doubt be found. The change from the Bridger will, however, almost certainly remain a very striking one in the reduction of these animals. They are not certainly known to occur in the White River, though some specimens have been referred to the group (*Laopithecus, Menotherium*).

CREODONTA.

MESONYX Cope.

M. UINTENSIS Scott (No. 16, pp. 168, 169); Pl. X, Fig. 9. The specimen upon which this species is founded consists of five isolated lower molar and premolar teeth, an incisor, a canine, one upper premolar and fragments of the mandible, including the condyle. The reference to *Mesonyx* is somewhat uncertain on account of the absence of the upper molars; there can be no doubt, however, that the species belongs to the family *Mesonychidæ*, and it is of interest as being the largest and latest known member of that long-lived and most curious group of creodonts. This species may be distinguished from those of the earlier Eocene formations by very much greater size and by the fact that the anterior basal cusps of the lower molars are much reduced.

The incisor is peculiar and consists of a broad and rounded simple crown; it is of large size and contrasts strongly with the incisors of the Bridger species *M. obtusidens;* the canine and upper premolar differ from the corresponding teeth of the

Bridger species only in size. Since the first account of this species was written, we have found that the order of the teeth was there incorrectly given; what was there described as the second premolar being probably the third molar. The most anterior premolar of the lower series preserved in the specimen is probably the second (see Pl. X, Fig. 9). This is a relatively small tooth, implanted by two fangs and with a low, rather elongated crown, which consists of a median cone and faintly separated anterior basal tubercles; this tooth is therefore somewhat differently constituted from the second lower premolar of *M. obtusidens*, in which the anterior tubercle is not indicated at all, and the posterior one scarcely so. The fourth premolar has nearly the shape and size of the true molars, consisting of a high and massive, backwardly directed principal cusp, which is separated by a deep and narrow cleft from the large trenchant heel. The latter is as long from before backwards as the main cusp and is strongly convex on the outer side and concave on the inner. This tooth differs from the fourth premolar of *M. obtusidens* only in the absence of the anterior basal cusp. The first true molar has the same construction as the tooth just described, but is larger, and the main cusp is remarkably massive; there is an indication of the anterior basal cusp, but it is much less distinctly marked than in the Bridger species. This tooth is the largest of the series and considerably exceeds in size the lower sectorial of a full-grown lion. The second molar differs from the first only in being a little smaller and in the still greater reduction of the anterior basal cusps. The development of these cusps varies greatly in the different genera of the family; in *Dissacus* of the Puerco they are fairly well developed; in the Wasatch genus *Pachyœna* they are greatly increased in size, becoming as large as the heel, which gives the inferior molars a trifid appearance when seen from the side. In the Bridger species of *Mesonyx* these cusps become much smaller, being greatly exceeded in size by the talon, while in *M. uintensis* they have almost disappeared, entirely so in fact, from the fourth premolar. The third molar is very small, and is even more reduced in size than in *M. obtusidens*, which reduction chiefly affects the talon; in the Bridger species the talon is of good size, but in the specimen before us the heel is a mere rudiment. The main cusp is also more compressed and pointed. The third molar is very differently developed in the various genera of the family; in *Dissacus* and *Pachyœna* $\overline{m.\ 3}$ is nearly or quite as large as $\overline{m.\ 2}$; in *Mesonyx obtusidens* it is distinctly smaller, the proportions being $7:9$, and in *M. uintensis* it is still smaller, as $3:5$. This reduction in *Mesonyx* is, of course, correlated with the loss of the last upper molar, and the proportions in the Uinta species would seem to indicate that the second upper molar was undergoing a similar reduction.

It has been generally assumed that the molar teeth of the *Mesonychidœ* are of

an exceedingly primitive pattern. As far as the upper molars are concerned this is no doubt true, these teeth never varying from a simple tritubercular pattern. *Dissacus*, however, shows that the lower molars were originally of the tuberculo-sectorial pattern, as the postero-internal cusp is distinctly present, from which it follows that the simplicity of the *Mesonyx* molars has been attained by the suppression of parts, somewhat in the same fashion as has been done in the lower sectorial of *Hyænodon* and the *Felidæ*. These lower molars of *Mesonyx* can, however, hardly be called sectorial, as the shearing action is limited by the small height of the outer tubercles of the upper molars. The cusps of the lower series are, therefore, worn upon the summits and very rapidly become blunted and worn down.

A second specimen, consisting of parts of two metatarsals and a phalanx, should probably be referred to this species, as their shape and character are very similar to those of *M. obtusidens*. The latter species is remarkable for the small size and weak development of the feet, but if these bones from the Uinta are correctly referred, *M. uintensis* must have had very different proportions, for they are considerably shorter and much more massive than in the lion. It is obvious that the Uinta *Mesonyx* must have been a very formidable animal, much more so than the more highly organized carnivores and creodonts (except *Hemipsalodon*) which succeeded it in the White River epoch.

Measurements.	*M.*
Diameter of incisor (fore and aft)	.011
" " (transverse)	.011
Diameter of canine	.022
Length second lower premolar	.014
" fourth " "	.028
Thickness " " "	.012
Length lower molar series	.078
" first molar	.031
Thickness first molar	.015
Length second "	.029
Thickness second molar	.015
Length third "	.018
Transverse diameter of mandibular condyle	.037

MIACIS Cope.

This genus of creodonts is the one which most closely approximates the true Carnivora and is characterized by the sectorial pm. 4 and m. 1. This is also true of *Didymictis*, but here the last upper molar is wanting and the lower sectorial is of very different character.

? MIACIS VULPINUS S. & O. (Syn. ? *Amphicyon vulpinum* S. & O., No. 17, p. 255). Since our preliminary account was written we have had the opportunity of examining various specimens of *Amphicyon*, which show that our tentative reference of the Uinta species to that genus must have been incorrect. It is equally clear that the species cannot belong to *Cynodictis*, or to any of the flesh-eaters known to occur in the White River beds, whereas it may very well be a species of *Miacis*, and in view of the similarity of the Uinta fauna to that of the Bridger, this will probably turn out to be the case. The specimen consists of an isolated inferior premolar and first molar.

The premolar, probably the third, consists of a high, acute and compressed cone, with rudimentary posterior heel; a cingulum runs entirely around the crown and is most conspicuous on the anterior surface. The principal cusp is not complicated by the development of accessory tubercles upon it. The sectorial is canine in appearance; the anterior portion consists of three cusps arranged in the ordinary triangle, of which the external is the larger and flattened on the outer side; the anterior cusp is still very low and the sectorial blade is therefore much less completely developed than in *Cynodictis* and hardly more so than in the Bridger species of *Miacis*. The heel of the sectorial is low and small and not very distinctly basin-shaped.

RODENTIA.

PLESIARCTOMYS Bravard.

Of all the rodents of the American Eocene, this genus is by far the most abundant and characteristic, being found in all of the formations above the Puerco, which indeed has hitherto yielded no rodents at all.

This genus has been defined by Cope (No. 3, p. 175-6) as follows: " The crowns of the inferior molars support four rather small and strictly marginal tubercles, which inclose a median valley. The anterior inner tubercle is more elevated than the others, and the posterior two tubercles are connected by a low ridge on the posterior border, which may be more or less tubercular on the last molar. In some of the species the marginal tubercles are merely elevations of the margin, while, in others, the adjacent tubercles of a pair approximate, so as to form a pair of interrupted cross-crests.

" There are five superior molars, of which the anterior is of small size. They resemble those of *Sciurus*, but the transverse crests are obsolete or wanting. The positions corresponding to their external extremities are marked by more or less dis -

tinct cusps. There is a single internal tubercle of the crown. In the third and fourth molars of *P. delicatissimus*, I observe rudiments of a second internal tubercle.

" The incisor teeth are compressed, with narrow anterior face. The enamel is not grooved and is little or not at all inflected on the inner side of the shaft, while it is extensively so on the external face. There is a large round *foramen infraorbitale* like that of *Ischyromys* and *Fiber*, and entirely unlike that of *Gymnoptychus* and *Sciurus*, conforming in this respect to the forms of the extinct group of the *Protomyidæ* of Pomel."

PLESIARCTOMYS SCIUROIDES S. & O. (Pl. XI, Figs. 1–2). The specimen upon which this species is founded consists of a skull, lower jaw and several limb-bones. It differs from the Wasatch and Bridger species principally in the character of the superior molar teeth, in which the transverse crests, wanting in the earlier members of the genus, are clearly though not very prominently developed. There are also several differences of minor importance in the structure of the skull. These characters may possibly be regarded as of generic value, but the changes are so slight and the agreement with the typical species of *Plesiarctomys* so close, that we do not feel justified in forming a new genus. In size the Uinta species is very small, much inferior to *P. delicatissimus.*
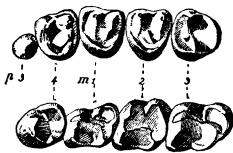
The *skull* is very much like that of the last-named species, but with some not unimportant differences. The muzzle is rather shorter, though both longer and broader than in *Sciurus;* the nasal bones are considerably broader behind than in front, thus reversing the proportions found in *Arctomys ;* their anterior ends are somewhat thickened and slightly divergent, and posteriorly they terminate on the same transverse line as the premaxillaries; the latter are quite large and exhibit a considerable surface upon the dorsal side of the skull. The frontals have a broad and nearly straight anterior edge, but narrow very rapidly, showing a very strong postorbital constriction of the cranium and no trace of postorbital processes, as is the very general rule among the more ancient rodents; they also seem to have a smaller anteroposterior extent than in *Sciurus*, though this cannot be definitely decided. This portion of the skull has quite a different aspect from that seen in the two other species, of which the structure of the cranium is known, *P. delicatissimus* and *P. hians.* It differs from the former in that the postorbital constriction is less decided and less elongated from before backwards, while the frontals are much more widely expanded in advance of the constriction and over the orbits; the superciliary ridges seem also to be somewhat more prominent. So far as one can judge from Cope's figure (No. 3, Pl. XXIV, Fig. 5) the postorbital constriction is deeper and the cranium more tapering in front in *P. sciuroides* and *P. hians.*

As in the other species the infraorbital foramen is in the species before us large and situated more immediately beneath the orbit than in *Sciurus*. The shape of the lachrymal cannot very well be made out. The parietals are apparently very long; they are broader than in *Arctomys*, narrower than in *Sciurus*, and the sagittal crest is barely indicated. The squamosal has, of course, a corresponding development; the zygomatic arches are very slender and compressed; they do not arch out very strongly from the sides of the cranium and are somewhat shorter than in *P. delicatissimus*. The anterior part of the arch is shaped much as in *Sciurus*, but the jugal has a somewhat greater vertical depth.

The occiput is very broad and low; in the median line it forms a slight convexity over the vermis of the cerebellum, and on each side of this there is a rather deep depression. The paroccipital processes are very short, and the *foramen magnum* very large. The base of the skull is much injured, but enough is preserved to show that the basi-occipital is rather broad and flat, and that the tympanic bullæ are moderately inflated. The posterior nares are rather long and their anterior edge extends to the front of the last molar; in *Sciurus* and *Arctomys* it is altogether behind the molar series. The mandible is relatively more robust than in *P. delicatissimus;* the masseteric fossa is, however, not so deep, and extends forward to beneath the second molar; the coronoid process is shorter, more slender and pointed, and the notch between it and the condyle is not so deep.

The *brain* is in general like that of *P. hians*, but the cerebellum is proportionately larger, the hemispheres shorter, broader behind and tapering much more rapidly forwards; the olfactory lobes are also narrower.

The *Dentition*. The molar formula of this species, like that of the other members of the genus is pm. $\frac{2}{1}$, m. $\frac{3}{3}$. In the upper series the penultimate premolar (pm. 3) is implanted by a single fang and has a very small and simple crown, thus differing strongly from the large pm. 3 of *Arctomys*. Pm. 4 is nearly as large as the molars. The crown is of triangular shape and consists of three tubercles at the angles of the crown, with a fourth one intercalated between the internal and postero-external cusps, thus forming an interrupted posterior crest; the antero-external cusp is the

DIAG. 1.—Upper and lower molars of *P. sciuroides.* × $\frac{2}{1}$.

largest and most prominent of the three. This tooth resembles much the corresponding one of *Arctomys*, but with the difference that the posterior line of tubercles have not coalesced to form a crest and that the cingulum is much less strongly developed on the front of the crown. The molars are very closely like those of *Sciurus*, but of more distinctly triangular shape. In m. 1 and 2 there are two external cusps from which

run two crests, meeting at the internal cusp and thus forming a V. In *Sciurus* the crown is somewhat expanded behind the posterior crest, thus making the inner side of the tooth nearly as broad as the outer; in *P. sciuroides* this expansion is much less marked. M. 3 has but a single transverse crest with a broad basin-like expansion behind it. The upper molars of *Plesiarctomys* are obviously of the same fundamental type as those of *Sciurus* and *Arctomys*; their chief difference from the latter consists in the fact that the cingulum on the anterior side of the crown is not strongly developed and is scarcely visible from the side, whereas in *Arctomys*, this portion of the cingulum is very prominent and gives the side view of the tooth an appearance of being composed of three distinct transverse crests.

The lower teeth are much worn, and it is therefore rather difficult to analyze their construction. The single premolar is composed of a pair of anterior cusps, of which the inner one is high and pointed, the outer one very small and but faintly distinguished from its neighbor, and a low heel. The molars have four cusps surrounding a median depression, of which the antero-internal one is much the most prominent. The presence or absence of connecting crests could not be clearly made out. The resemblance of these teeth to the lower molars of *Sciurus* is very close.

The *humerus* is short and very slender with large head and low, inconspicuous tuberosities; the bicipital groove is distinctly deeper than in *P. delicatissimus*, and the deltoid ridge is quite long and prominent. The distal end of the specimen is broken, but enough remains to show that the epicondylar foramen is present and that the supinator ridge is somewhat less prominent than in the Bridger species so frequently referred. Whether the Uinta species had such a prominent internal epicondyle is not certain.

The *tibia* is quite long, slender, and strongly arched forwards; the distal end is quite deeply grooved for the astragalus and the internal malleolus is well developed. The fibula, although not preserved in the specimen, was evidently entirely distinct, as the outer face of the distal end of the tibia is uninjured and exhibits no trace of coössification with the fibula.

Measurements.   *M.*

Length of skull	.061
Breadth of skull in front of orbits	.025
" " behind "	.010
Length of lower jaw	.028
Length upper molar series	.013
" lower " "	.012
Antero-posterior diameter of lower incisor	.003
Transverse " " "	.002
Length of humerus (estimated)	.043
" of tibia	.066

The chief interest which attaches to *Plesiarctomys* lies in the light which it throws upon the difficult problem of the origin of the rodent dentition. As to this question Schlosser says: "Die Zähne dieser ältesten Formen erinnern einigermassen an das *Omnivoren*-Gebiss. Doch lässt sich die ursprüngliche Beschaffenheit nicht mehr ermitteln. Wahrscheinlich bestand der einzelne Backzahn aus sechs Hügeln ('Denticules'), deren je drei in einer Zahnhälfte vorhanden waren. Der Typus eines solchen *Primitiv-Omnivoren*-Zahnes ist noch am besten in den oberen Molaren von *Dichobune* erhalten. Hier tritt nicht selten noch der sechste Hügel auf, worauf schon Kowalevsky aufmerksam gemacht hat. Bereits zu Anfang der Eocaenzeit erscheint eine grosse Anzahl verschiedener Näger, die indess nur insoferne unter einander verwandt sind, als sie mit Ausnahme von ganz wenigen Arten—*Myomorpha*—als Mittelformen zwischen den in der Jetztwelt ziemlich scharf getrennten *Hystricomorphen* und *Sciumorphen* angesehen werden müssen. Auch fehlen keineswegs Mittelformen zwischen diesen und den *Myomorphen*" (No. 14, pp. 98–99). After a further discussion of the subject Schlosser concludes that the rodents are to be derived from the marsupials.

Plesiarctomys lends but little support to these views, and this genus is entitled to special consideration as being one of the oldest if not the very oldest known form of rodent. Here the superior molars are plainly of the tritubercular pattern, forming distinct crests only in the later species. The inferior molars show the anterior triangle of three cusps with a talon behind, or what Cope has termed the tuberculo-sectorial molar. This is the type of dentition which is all but universal in the Puerco fauna, ungulates, creodonts and lemuroids all exhibit it, and *Plesiarctomys* seems to show that the rodents are to be derived from the same generalized group of primitive placental mammals, the Bunotheria, to which we refer the origin of the types just mentioned. It is, to say the least, very suggestive that the most ancient known types of rodents should exhibit the tritubercular plan of molar structure so unmistably, though it must be admitted that this of itself is not conclusive against their derivation from the marsupials. It removes, however, the necessity of such a derivation, and the other reasons assigned by Schlosser for his view do not appear to be very cogent.

Plesiarctomys is, on the whole, to be regarded as a member of the Sciumorpha, but certain features, such as the large infraorbital foramen and the absence of postorbital processes, are points of resemblance to the Hystricomorpha. This association of characters, as is shown in the passage already quoted from Schlosser, is very generally found to occur in the Eocene rodents.

ARTIODACTYLA.

LEPTOTRAGULUS S. & O.

Our preliminary account of this genus was founded upon the mandible and inferior dentition. Since then a considerable amount of new material has been brought to light in the collection which materially modifies some of our conclusions. The genus may be thus defined: Selenodont artiodactyls with probably unreduced dentition; lower premolars simple and trenchant; molars with short crowns; the crescents of the lower molars are more or less trihedral, and the internal ones not flattened into thin laminæ. The ulna and radius closely applied, but not coalesced; the number of functional digits in the manus probably four, in the pes two.

LEPTOTRAGULUS PROAVUS S. & O. (Pl. VII, Figs. 9-16). This species, the only one as yet certainly indicated from the Uinta deposits, is represented in the collection by several specimens, including the mandible, inferior molar series and last premolar, some fragments of vertebræ and portions of the humerus, ulna and radius, metacarpus, phalanges, scapula, tibia, tarsus and metatarsus. Imperfect as these remains are, they suffice to show the principal characters and systematic position of the genus with sufficient clearness. Unfortunately no part of the skull or of the upper teeth has as yet been identified.

The *Mandible.* Only the horizontal ramus is preserved in any of the specimens; this is elongated, compressed and slender, becoming especially thin beneath the anterior premolars, and thus offering a strong contrast to the short deep mandible of *Protoreodon* with its abrupt chin. The symphysis extends back nearly as far as the front of the second premolar; two minute venous foramina are placed, one above the other, beneath the third premolar.

Dentition. The fragmentary state of the specimens prevents the determination of several important points with reference to the lower teeth of this genus. Thus, the number and character of the incisors and canines are altogether uncertain, though probably they were present in full. In front of the third premolar is a short diastema, and in advance of this occurs a pair of obliquely placed alveoli, which may have contained the first premolar, or the canine and lateral incisor, which latter view seems the more probable on account of the procumbency indicated, though this would necessitate an exceedingly short symphysis. In this case, the number of lower premolars would be but three. The premolars are very simple and trenchant, and in general appearance quite like those of *Tragulus.* Pm. 2 has a very compressed and sharply trenchant crown; it has a sharper posterior edge than in *Tragulus* and is apparently not divided, as in that genus, by a cleft. Of pm. 3 only the fangs are left. Pm. 4 is slightly

more complicated than its predecessors; it consists of a high, acute, and compressed cone with a small and sharp antero-internal tubercle; from the inner side of the apex of the principal cusp there runs downwards and backwards a thin ridge, which encloses a very narrow valley between itself and the outer posterior edge of the crown. The corresponding tooth in *Tragulus* has quite a different appearance.

The molars are very brachyodont and are rather short in the antero-posterior direction; the inner cusps are conical and thick, not flattened out into thin plates; the outer crescents are somewhat trihedral in section and rather angular than curved. The valleys are widely open at the top, but rapidly narrow below, becoming mere slits after a moderate degree of attrition. The two valleys of the same tooth are not quite connected, being separated by the deep constriction between the two outer crescents and by the coalescence of the posterior turn of the anterior crescent with the inner wall of the tooth. They are, however, closely adjacent and even in an advanced stage of wear do not become widely separated. The cingulum is quite strongly marked upon the anterior and posterior faces of the crown, as well as between the outer crescents, where it forms a distinct accessory column, which is largest on the first molar. The heel of the last molar is relatively large and encloses a broad valley; a narrow cleft appears upon its inner wall.

The teeth associated with the skeletal fragments about to be described are so much damaged that their reference to this genus is not quite certain, though very probable; they are somewhat larger than those of the type specimen, and may, perhaps, represent a second species.

Vertebræ. An isolated atlas is probably to be referred to this genus. It just reverses the proportions of the atlas of *Protoreodon* in being long and narrow, and with but slightly extended transverse processes; between the anterior and posterior articular surfaces the body of the vertebra is deeply constricted. The anterior cotylus for the occipital condyle is very deep and transversely extended, narrow from above downwards, and is slightly notched on the outer edge. The transverse processes are thin plates and do not appear to be perforated at the base by the vertebrarterial canal. The surfaces for the centrum of the axis are flat, oval and placed almost transversely; there is no facet upon the posterior edge of the inferior arch of the atlas, for the centrum of the axis beneath the odontoid process, such as occurs in the camels and true ruminants. Fragments of other vertebræ occur in the collection, which undoubtedly belong to *Leptotragulus,* but they are not sufficiently well preserved to warrant description.

Of the *scapula,* the distal portion is preserved. The glenoid cavity is oval in shape, the antero-posterior diameter exceeding the transverse; the coracoid is promi-

nent and but little recurved. The position of the spine is somewhat different from that seen in the recent selenodonts, in which the spine is placed in advance of the median line, thus making the prescapular fossa much smaller than the postscapular. This inequality is also shown in a less degree in *Leptotragulus*, in which respect this genus agrees with the earlier selenodonts, such as *Anoplotherium* and *Oreodon*.

Of the *humerus* we have only the distal end, which, however, shows some interesting characters. The internal epicondyle is not prominent and is pushed to the posterior side; the inner condyle of the trochlea is much extended transversely, while the outer condyle is narrow; the intercondylar ridge is not prominent, and is above rounded and rather broad, but rapidly becomes narrow and sharp. This portion of the humerus forms a strong contrast to that of the oreodonts, which finds a parallel only in *Anoplotherium*. The anconeal fossa is deep and narrow and appears to perforate the shaft.

The *ulna* and *radius* are very closely applied together, but they do not coalesce, at least in the proximal portion, whatever may be true of the distal end. The ulna has a heavy and prominent olecranon and a deeply incised sigmoid notch, with a recurved superior margin. The contact with the humeral condyles is limited to very small inner and outer facets, which are but continuations backwards of the corresponding radial facets. The shaft is quite broad at the level of the head of the radius, but rapidly tapers below this point and becomes very slender and reduced. The head of the radius is both broad and deep; it is only slightly concave, and the division into facets only obscurely marked; the anterior margin rises somewhat towards the inner side; the groove for the intercondylar ridge is very shallow, and the front margin is not notched. Below the head, the shaft tapers and becomes more rounded. Unfortunately neither the distal ends of the forearm bones, nor any of the carpal elements, have been found.

The *femur* is represented by a much damaged proximal end, which, however, presents some interesting features. The head is small, hemispherical, and set upon a long and very distinct neck; the pit for the *ligamentum teres* is but faintly marked. The great trochanter is broken away, but it was obviously large and, with the strongly projecting neck, makes this region of the bone unusually broad. The second trochanter is large, rugose and prominent; what appears to be the remains of a ridge, connects this trochanter with the greater one, as in *Hyopotamus*, to the femur of which this fragment bears considerable resemblance. The shaft is broad and flattened above, but appears to taper rapidly and to become more rounded below.

Of the *tibia* we have only the distal end, with fragments of the proximal condyles, which, however, are too much injured for description. The lower portion of

the shaft is transversely extended and quite massive, expanding but little into the distal end. The articular surfaces for the astragalus are quite deeply incised and separated by a prominent intercondylar ridge. The outer edge of the distal surface shows a narrow facet for the fibula, indicating that the latter had commenced to shift beneath the tibia; though the narrowness of this facet and the large rugose surface upon the external side of the tibia, make it probable that the reduction of the fibula was by no means complete. It has, however, clearly begun.

The foot structure of *Leptotragulus* is very curious, though we are unfortunately not in a position to give a complete account of it. The *manus* seems to have possessed four functional digits, and is represented in the specimen before us by the proximal ends of what appear to be the second and fourth metacarpals. Mc. II (?) is slender, but hardly more reduced than in *Oreodon*. Its proximal end shows three facets, of which the largest is a concave one for the trapezoid, and behind this a separate one for the trapezium; a small oblique surface towards the ulnar side seems to be for the magnum, thus indicating an "unreduced" type of manus. Mc. IV is much stouter and has a trihedral shaft and a simple, saddle-shaped surface for the unciform. On the ulnar side is a deep depression, apparently for the fifth metacarpal. This account is given with reserve, as the fragments described are too imperfect for certain identification, and the differences indicated between the fore and hind foot are very remarkable.

The *pes* is fortunately much better preserved than the manus. The calcaneum is rather long, compressed and deep, with approximately parallel edges. The fibular facet is prominent, strongly arched from before backwards and descending abruptly in front. An astragalar surface is on the inner side of this facet and forms a sharp angle with it. The distal end of the calcaneum is very narrow, but of considerable antero-posterior extent, and bears upon its inner side an unusually large surface for the astragalus. The latter is strikingly high and narrow; the proximal condyles are small and quite widely separated; the outer one is divided by a considerable interval from the cuboidal facet, while the inner extends further down and reaches the navicular surface. The fibular facet upon the outer condyle is very long. The distal trochlea is unevenly divided between the facets for the navicular and cuboid, the latter being very narrow. The inferior surface for the *sustentaculum tali* is long and narrow and separated by a deep pit from the overhanging external proximal condyle. The cuboid is high, narrow, and deep (antero-posteriorly); the calcaneal facet is arched from before backwards and in front descends much below that for the astragalus; it is also slightly broader than the latter; upon the tibial side of the cuboid are two small and widely separated facets for the navicular, the position of which indicates that the

latter bone was comparatively low, and the cuneiforms high. The distal end is entirely occupied by the large facet for metacarpal IV, though what seems to be a small facet for mt. V occurs upon the external side. The posterior hook-like process of the cuboid is long, heavy and recurved.

The metatarsus apparently consists of two functional members, though grooves and facets upon the sides of these indicate the presence of at least the proximal portions of the lateral metatarsals. Mt. II appears to have been less reduced than mt. V. The median pair are more slender than the corresponding metacarpals, and were probably more elongate; their shafts are flattened and the approximate surfaces very closely applied, but show no tendency to coössify; both have strong posterior projections from the proximal ends. The head of mt. III would seem to indicate that the meso and ectocuneiforms were not coössified. Mt. IV covers the entire distal surface of the cuboid, allowing to mt. V only a lateral connection with that bone. The distal ends of the median metatarsals at once suggest the characteristic cannon-bone of the Tylopoda, and are remarkably like those of the White River representative of that group, *Poebrotherium*. The articular surface is but slightly marked off from the shaft, and the keel, though prominent, is confined entirely to the palmar side. When the ends of the two metatarsals are placed together they exhibit a slight divergence, as is the case in a much more marked degree in the recent Tylopoda.

The *phalanges* of the proximal row are long and slender and curved outwards; the proximal surfaces are somewhat symmetrical, causing a slight divergence of the toes. The ungual phalanges are high, compressed and pointed, and somewhat flattened on the internal (approximate) sides; they resemble the unguals of the antelopes much more than those of recent Tylopoda.

The Systematic Position of Leptotragulus.

In our preliminary account, drawn up from the mandibular dentition only, we inclined to the view that this genus was allied to *Prodremotherium*, and was, perhaps, the forerunner of the White River *Leptomeryx*. The new material identified since that description was written, as well as direct comparison with original specimens of *Prodremotherium*, shows that our former conjecture is entirely untenable. The teeth, and still more strongly the skeletal fragments, prove that *Leptotragulus* is very closely allied to *Poebrotherium*, and is, therefore, the earliest known representative of the Tylopoda. If more perfect specimens should confirm the doubtful indication in the type of the loss of the first lower premolar, this species, at least, could not be placed

in the direct line of descent, though in any event it is but slightly removed from that line.

The inferior premolars are composed of the same elements as in *Poebrotherium*, but have quite a different appearance, owing to their moderate antero-posterior extent, while in the latter genus they are very much elongated; the difference between the two being least marked in the case of the last premolar. The most important distinction in the molars of *Leptotragulus* from those of the White River genus consists in their completely brachyodont character; they are also not so far removed from the bunodont pattern; the inner cusps are stout and conical, and the outer distinctly trihedral, while in *Poebrotherium* the crescents, and especially the internal ones, are compressed into thin laminæ. The crescents are not so sharply separated by deep constrictions, and the valleys are more nearly confluent in the Uinta genus; the heel of the last molar is also proportionally larger and contains a deeper valley. Another difference consists in the absence from the molars of *Poebrotherium* of the small columns developed from the cingulum between the outer crescents. The elongated slender shape of the mandible recalls that seen in *Poebrotherium*.

The atlas is almost a reduced copy of that of *Poebrotherium*, but the notch at the side of the anterior cotylus is not nearly so deep, and there is no articular surface developed on the hinder edge of the inferior arch to connect with the centrum of the axis below the odontoid process.

The scapula has a more oval glenoid cavity, a less prominent coracoid, and the spine is placed more nearly in the median line; the intercondylar ridge of the distal end of the humerus is narrower and less prominent.

If we may trust the account given above, the manus is very different in the two genera in that the manus of *Leptotragulus* is but slightly reduced, and that the second metacarpal retains its connection with the magnum. The fibula seems also to be less reduced, though the process has obviously begun. The tarsus, metatarsus and phalanges are much like those of *Poebrotherium*, with only slight differences, such as the larger size of the cuboid hook and the relative narrowness of that bone. The unguals are very closely alike in the two genera, and indicate that the peculiar foot structure which characterizes the camel and llama could not have occurred in the Uinta and White River representatives of the group, which probably had feet with the general appearance of those of the ordinary ruminants. The pad or cushion developed, no doubt, *pari-passu* with the formation of the peculiar cannon-bone with its diverging distal ends. The ungual phalanges of *Protolabis* and *Procamelus* have not as yet been identified, but there is every reason to suppose that they exhibit successive stages of reduction.

Leptotragulus is, therefore, to be regarded either as the direct ancestor of *Poebrotherium*, or as very closely connected with that ancestor. Unless, however, the doubtful indications of tetradactyl feet in the Uinta genus should be confirmed, it throws no great amount of light upon the vexed question of the origin of the camels and their relations to other selenodonts. Among the imperfectly known and sparsely represented artiodactyls of the Bridger, the one which most clearly suggests itself as a forerunner of *Leptotragulus* is *Homacodon*. This animal is described by Marsh (No. 9, p. 364) as being "very nearly allied to *Helohyus*, and but a single step away from this genus towards the selenodonts. * * * This primitive selenodont had forty-four teeth, which formed a nearly continuous series. The molar teeth are very similar to those of *Helohyus*, but the cones on the crowns have become partially triangular in outline, so that when worn the selenodont pattern is clearly recognizable. The first and second upper molars, moreover, have three distinct posterior cusps, and two in front; a peculiar feature, which is seen also in the European genera, *Dichobune* and *Cainotherium*. There were four toes on each foot, and the metapodial bones were distinct. The type species of this genus was about as large as a cat. With *Helohyus* this genus forms a well-marked family, the *Helohyidæ*."

The association of these two genera into a single family is quite inadmissible, as it ignores a fundamental difference in the construction of the upper molars; in *Helohyus* the fifth cusp is in the anterior half of the tooth, while in *Homacodon* it is in the posterior half. This latter genus belongs clearly to the *Dichobunidæ*, and the published description shows no reason for separating it from *Dichobune* itself. Before identifying it with the European form, however, it seems best to wait for fuller information with regard to the American species. Similarly, in the absence of the upper molars, it would be premature to state that *Leptotragulus* is to be derived from *Homacodon*, though there is nothing in what is known of the two genera to forbid such a derivation, which may therefore be fairly assumed. If this connection should be confirmed, it would necessitate revision of the current views upon the relationships of the Tylopoda. Schlosser (No. 13, p. 42) regards this group as a branch of the same general stem which developed the *Anoplotheridæ*, the *Anthracotheridæ*, etc., and especially as being connected with the oreodonts, a suggestion which has also been made by Rütimeyer (No. 11, p. 98). On the other hand, Schlosser derives the tragulines and true ruminants from the *Dichobunidæ*, thus making a very radical distinction between the Tylopoda and the other existing selenodonts. If, however, the suggestion here made, that *Homacodon* and *Leptotragulus* are genetically connected, be confirmed, it follows that the Tylopoda are also to be derived from the *Dichobunidæ*, and therefore from the same origin as the other recent selenodonts. Such a result would

further conclusively demonstrate that the oreodonts are but remotely connected with the camels, as is indeed made exceedingly probable by what we already know of the earlier members of the two groups. *Protoreodon*, which will be fully described hereafter, shows the unpaired cusp in the anterior half of the upper molars, just as in *Helohyus*, from which, indeed, it seems to have been derived, and its resemblance to such types as *Anoplotherium* and the (so-called) Eocene species of *Hyopotamus* is very marked, and Schlosser is fully justified in associating the oreodonts with these phyla. On the other hand, the resemblances between the camels and the oreodonts are only such as are common to all the more primitive selenodonts, and indeed this peculiar family has decidedly more similarity to the tragulines than to the camels. *Leptotragulus* is almost as different from its contemporary *Protoreodon*, as *Oreodon* is from *Poebrotherium*, or *Merychyus* from *Procamelus*. The Bridger representatives of these two phyla are apparently *Helohyus* and *Homacodon*, which not improbably take their rise from a common starting point in *Pantolestes* of the Wasatch, which would thus be the progenitor of the two characteristically American groups of selenodonts, as well as through the *Dichobunidœ* of the European series also. Of course, in the present state of knowledge, these suggestions can only be made tentatively ; they are not yet capable of demonstration.

Whether we adopt the scheme of genetic relationships propounded by Schlosser, or the one here suggested, it necessarily follows that the word *selenodont* can only be used as a term of description and not of classification ; for it seems clear that this pattern of dentition has been independently assumed by many groups of artiodactyls. Nearly all the types of selenodonts may be traced back step by step to the generalized buno-selenodonts of the Eocene, and the resemblance between the molar teeth of such forms as *Tragulus* and *Cainotherium*, *Oreodon* and *Cervus* is much more probably due to mechanical conditions than to genetic relationship.

Measurements.	M. * Homacodon vagans.	M. † Leptotragulus proavus.	M. Poebrotherium wilsoni.
Length lower premolar series (last three).....		.021	.030
Last lower premolar antero-post. diameter.....		.007	.011
" " " transverse "		.003	
First lower molar antero-post. diameter........		.008	.011
" " " transverse "		.005	.006
Length lower molar series...................	.017.5	.026†	.042
Last lower molar antero-post. diameter.......	.007.3	.012†	.019
" " " transverse "	.004	.006†	.007
Height of astragalus.......................	.014	.020	

* These measurements from Marsh, Am. Jour. Sci. and Arts (3), IV, p. 126.
† Second specimen.

PROTOREODON S. & O. (Pl. VII, Figs. 1–8).

This genus is the most perfectly known and after *Triplopus* the most abundant of all the Uinta mammals. The Princeton collection contains portions of a large number of individuals representing nearly all the important parts of the skeleton and pertaining apparently to two species. The genus is to be defined as follows: "Selenodont Artiodactyla with unreduced dentition; inferior canines with the form and function of incisors, first lower premolar caniniform; superior molars of five crescents, the unpaired one much reduced and situated in the anterior half of the crown, outer wall erect and flattened; crowns very low and broad, valleys widely open; inferior molars much like those of *Agriochœrus* with conical internal crescents. No diastemata in lower dental series and a very short one behind the upper canine. Cranium narrow and very much elongated, orbit open behind, apparently no lachrymal pit. Lunar resting more directly upon the magnum than in *Oreodon;* manus pentadactyl; pes tetradactyl and inadaptively reduced.

Before proceeding to describe the osteology of this remarkable genus it may be well to glance at previous notices of the Uinta selenodonts. The first one described is the *Agriochœrus pumilus* Marsh (No. 8, p. 250), which is founded upon the inferior dentition. It seems highly improbable that this White River genus should occur in the Uinta, and the lower molars of *Protoreodon* being, as we have already seen, much like those of *Agriochœrus*, one is led to infer that this supposed *Agriochœrus* belongs to *Protoreodon,* but in the absence of the upper molars this cannot be certainly determined. Prof. Marsh (No. 9, pp. 364–5) subsequently named three genera from this formation, of which he says: "In the *Diplacodon* horizon of the Upper Eocene, the selenodont dentition is no longer doubtful, as it is seen in most of the *Artiodactyla* yet found in these beds. These animals are all small, and belong to at least three distinct genera. One of these, *Eomeryx,* closely resembles *Homacodon* in most of its skeleton, and has four toes, but its teeth show well-marked crescents and a partial transition to the teeth of *Hyopotamus* from the Eocene of Europe. With this genus is another (*Parameryx*), also closely allied to *Homacodon,* but apparently a straggler from the true line, as it has but three toes behind. The most pronounced selenodont in the Upper Eocene is the *Oromeryx,* which genus appears to be allied to the existing deer family, or *Cervidæ,* and if so is the oldest known representative of the group." "The least specialized, and apparently the oldest, genus of this group [the oreodonts] is *Agriochœrus,* which so nearly resembles the older *Hyopotamus,* and the still more ancient *Eomeryx,* that we can hardly doubt that they all belonged to the same ancestral line." "A most interesting line, that leading to

the camels and llamas, separates from the primitive selenodont line in the Eocene, probably through the genus *Parameryx*." Whether any of these genera includes the previously described *Agriochœrus pumilus*, we are not informed, but the reference to the resemblance between the dentition of *Eomeryx* and that of *Hyopotamus* and *Agriochœrus* may perhaps be taken to imply that the former is founded upon the superior dentition of *A. pumilus*, and may therefore be the same as *Protoreodon*. That *Parameryx* may be identical with *Leptotragulus* is suggested by the reference of the former to the camel line. However, these meagre accounts, with no species descriptions, and no accompanying figures, are insufficient for identification.

The osteology of *Protoreodon* is in most respects very similar to that of its White River successor, *Oreodon*, though in several respects it is more primitive and presents many interesting indications which serve to point out the line of descent through which this remarkable family has passed, as well as its relationships with other groups of selenodonts, both American and European.

The *skull*, which fortunately is in a fairly good state of preservation, presents some features of great interest. It resembles in general construction that of the *Oreodontidœ*, being in some respects like that of *Oreodon*, in others more like the skull of *Agriochœrus*, while, in several ways, it is more primitive than either. As a whole the skull is longer and narrower than in the Miocene forms, a statement which applies especially to the cranium and more particularly to the posterior region of it behind the postglenoid processes, the length of which region is to a remarkable degree greater than in the later genera of the group. The face, on the other hand, is rather short, the anterior edge of the orbit being above the first molar. The cranial and facial axes are in the same straight line, and the upper contour of the skull is also nearly straight, as it is not complicated by the development of large air sinuses in the frontal region. The sagittal crest is very long and prominent, the occiput low and narrow.

As is general among the *Oreodontidœ* the parietals have a very great antero-posterior extent and form with the squamosals almost the entire cranium; posteriorly they are very narrow, but become much broader in front of the squamosals, where they send down great processes to meet the alisphenoids. The high sagittal crest extends the entire length of the parietals. The occiput is rather strongly convex, but is low and narrow, as are also the exoccipitals, which do not extend upon the side walls of the cranium. The paroccipital processes are long and slender, and are much like those in *Agriochœrus*, but are further in advance of the occipital condyles and even more widely separated from the postglenoid processes than in that genus, the elongation of this region of the cranium being especially characteristic of *Pro-*

toreodon. From the crushed condition of this part of the skull it cannot very well be determined whether or not the periotic was exposed upon the surface, but in all probability it was. The frontals form but very little of the roof of the cranium, as they terminate just behind the orbits and are chiefly confined to the covering of the orbits and nasal cavity. The supraciliary ridges are prominent and diverge from the sagittal crest, as in *Oreodon*, terminating in long, overhanging postorbital processes, but, as in *Agriochœrus*, they do not reach the jugal and the orbits are widely open behind.

The squamosals are very large and form most of the side walls of the cranium; they articulate with the parietals both superiorly and anteriorly. The zygomatic processes are very long; the free portion is compressed laterally and quite slender, but the bases have a considerable antero-posterior extent, as in *Oreodon ;* the post-glenoid processes are less massive, and are less produced transversely and more vertically than in that genus. The glenoid cavity is also somewhat different; Leidy thus describes it in *Oreodon* (No. 7, p. 75): " The glenoid articulation exhibits a broad surface extending outwardly on the under part of the posterior root of the zygoma. Its fore part is nearly straight and horizontal transversely, and is moderately convex antero-posteriorly, inclining forward internally and backward externally. Postero-internally it descends upon a remarkably large and strong postglenoid tubercle, which is antero-posteriorly compressed, mammillary in shape." This description applies also to the glenoid cavity of *Protoreodon*, except that the surface has a smaller extent from before backwards, it is rather more strongly convex in front and is not produced into an elevation internally; the postglenoid process is also much less massive.

In correspondence with the great elongation of the cranium the zygomatic arches are very long; the jugal is long and quite slender and has but a rudimentary postorbital process, which is widely separated from that of the frontal; it is not notched to receive the anterior end of the zygomatic process, as in *Oreodon*, and has a somewhat greater extension upon the face than in that genus. The lachrymal, on the contrary, would seem to be smaller, and apparently had no depression or pit, though this statement cannot be made positively.

The base of the skull is unfortunately much injured and allows but little to be made out with regard to its structure. The alisphenoids are very large and have large pterygoid plates, which bound the much elongated posterior nares; the latter extends far forward between the molars and ends anteriorly in a pointed arch, so that both in shape and position it agrees closely with that of *Agriochœrus*, and is quite different from that of *Oreodon*. It cannot be ascertained, whether or not the tympanic bullæ were inflated, but we may infer that they were from the fact that such

inflation occurs both in *Agriochœrus* and in the oldest species of *Oreodon* which are found in the lowest horizon of the White River formation, the *Titanotherium* beds.

The maxillary resembles that of *Oreodon*, being very low beneath the orbit and extending up to the nasals in advance of the lachrymal; the alveolar portion is low throughout in correspondence with the exceedingly low crowns of the teeth, and even the portion of the maxillary which forms the side wall of the nasal cavity is proportionately lower than in the Miocene genus. The palatine processes are rather narrow, and a narrow incision occurs between the alveolus of the last molar and the palatine plate; this incision is also present in *Oreodon*, but is broader. The infraorbital foramen is situated above the penultimate (pm. 3), which is the position it occupies in *Agriochœrus*, while in *Oreodon* it is placed somewhat more anteriorly. Neither nasals nor premaxillaries are preserved in any of the specimens.

The mandible is short and deep, with an abruptly rounded chin and long, very steeply placed symphysis. The condyle is shaped very much as in *Oreodon*, but the coronoid process is more like that of *Agriochœrus* in being higher and more deeply separated from the condyle, and consequently less like that of the peccary. So far as can be determined the angle of the mandible was not so much thickened as in *Oreodon*; the two rami are not closely interlocked and even in old individuals show no tendency to coössification.

The *dentition* is of especial interest as it serves to connect the isolated and peculiar family of the *Oreodontidæ* with the other selenodonts of the American and European Eocene.

Upper jaw. The superior incisors are not represented in the collection, and only the fang of the superior canine; the latter, however, shows the characteristic D-shaped section seen in *Oreodon*, and doubtless the crown presented no important differences. The same statement applies to the most anterior premolar (pm. 1). The second premolar, seen from the outer side, resembles much the corresponding tooth in *Oreodon*, having a compressed conical crown with trenchant edges. Seen from below, however, it is more simply constructed, as the small internal accessory valleys are barely indicated, and the cingulum is but feebly developed. The third premolar is more transversely extended than the preceding one and has the external wall slightly concave, but is constructed essentially like it, and is consequently simpler than the same tooth in *Oreodon*. Leidy describes these premolars in *Oreodon* as follows (No. 7, p. 81): " The anterior three upper premolars are constructed after the same plan. They decrease successively in size and in the degree of development of their details of form, from the third to the first of the series. Their crown is a trilateral pyramid, with a pointed apex and a broad external cordiform

surface. The narrower internal surfaces appear as triangular inclined planes, sepa-
rated by a median acute ridge extending from the point to the base of the crown.
The anterior of the internal surfaces forms at the base a pair of shallow pouches, de-
fined by a double festoon. The posterior of the same surfaces forms a single and
larger pouch at the base of the crown, included by a single and thicker festoon. This
latter in the third premolar almost assumes the dignity of an additional lobe to the
crown, resembling the internal lobes of the true molars." In *Protoreodon* these fes-
toons are not more distinctly marked on pm. 3 than on pm. 2, being only very faint
elevations of the cingulum and single, not double, on the anterior part of the crown.
Pms. 3 and 4 are each implanted by three fangs, pms. 1 and 2 by two. The last pre-
molar has the form seen in *Oreodon* and the ruminants generally; it consists of two
crescents, an internal and an external and an internal, with a strong internal cingulum.
The outer crescent still retains the cordate shape and the trenchant edges seen in the
anterior premolars, and is considerably larger than the external crescents of the
true molars. The cingulum is not so strongly developed on the outer side, nor is the
external wall of the tooth so deeply concave as in *Oreodon*.

The anterior premolars of *Protoreodon*, with their great simplicity of construc-
tion, are decidedly more like those of *Agriochœrus* than those of *Oreodon*, but the
fourth premolar resembles that of the latter genus, while in *Agriochœrus* it has
reached an extraordinary degree of complication, having almost completely assumed
the molar pattern, and differing only in the rudimentary state of the postero-internal
lobe.

The molars of *Protoreodon* increase in size successively from the first to the
third; the crowns are very low and broad in proportion to their antero-posterior ex-
tent; the valleys are very shallow and widely open; the internal crescents are massive
pyramids, and the horns are very faintly marked ridges. The external crescents are
intermediate in character between those of *Oreodon* and of *Agriochœrus*, in being less
concave and overhanging and less deeply separated by an outward extension of the
median valley than in the latter, more so than in the former, with an additional
resemblance to *Oreodon* in the compressed shape of the buttress between the outer
lobes and in the faint convex ridge which runs up from the apex of these crescents.
The balance of resemblance, as far as the outer wall of the tooth is concerned, in-
clines therefore towards *Oreodon*, while the construction of the inner half of the crown
and the general appearance of the whole is more like that of *Agriochœrus*. A very
important difference from the molars of all the oreodonts hitherto known consists in
the presence of a fifth lobe situated in the anterior half of the crown; it is but
slightly separated from the antero-internal crescent, with which it is apparently

beginning to coalesce. These five-lobed upper molars are found among nearly all the selenodonts of the American and European Eocene, and the discovery of *Protoreodon* confirms Schlosser's conjecture (No. 13, p. 42) that the *Oreodontidæ* have been derived from animals with molars of this pattern, though this ancestral type is clearly not what he supposed it would be, namely, the common form from which both oreodonts and Tylopoda have descended.

Lower jaw. The incisors increase in size from the median to the lateral one; their crowns are proportionately higher than in *Oreodon* and of somewhat different shape, in that they are more flattened and quadrate in outline and the cutting edges are straighter. In the median one the cutting edge is placed nearly at right angles to the lateral edges, while in *Oreodon* the incisors are more acute and pointed. As in all the later members of this family, except *Pithecistes*, the lower canine has assumed the form and functions of an incisor, and forms the largest of that series, while the first premolar has become caniniform, a transformation which is entirely peculiar to this line of selenodonts. Analogous changes occur in *Xiphodontherium*, where pm. 2 is caniniform, and in *Hypisodus* where the canine and first two premolars have gone over to the incisor series, but only the oreodonts show the enlargement of the first premolar and such a change of shape, that it almost deserves the name of a tusk. In *Protoreodon* the caniniform premolar is directed upwards and outwards, scarcely at all forwards; the outer side is quite strongly convex, the inner side is divided by a ridge, running down from the acutely pointed apex, into two somewhat concave surfaces, of which the anterior is somewhat the larger; the anterior and posterior edges of the crown are sharp and trenchant. In *Oreodon* both the outer and inner sides of the crown are more flattened; that is to say, in *Protoreodon* the transformation is less complete, the tooth retaining very clear marks of the fact that the functional canine is in reality a premolar. The other premolars have considerable resemblance to those of *Oreodon*, but are of less complicated construction and are more compressed and trenchant. Pm. 2 is a simple compressed cone, with very small transverse and considerable antero-posterior diameter; on the hinder edge is a very narrow and shallow depression, which is much more marked in *Oreodon*, but not in *Agriochœrus*, where this tooth is entirely simple and reduced in size. Pm. 3 is an enlarged copy of pm. 2, except that the internal cingulum is more pronounced and the posterior valley somewhat larger. In *Oreodon* this tooth is proportionately much larger, the valley is enlarged, curved inwardly and completely enclosed; the anterior half is also much more strongly concave on the inner side. Pm. 4 is more or less broken in all the specimens, but enough remains to show that it was more simply constructed than in *Oreodon*, which Leidy thus describes: " From the median point

an oblique ridge descends internally and terminates in a large trilateral pointed tubercle which springs from the middle of the base of the crown and rises nearly as high as the principal point." In *Protoreodon* this tooth has a very much smaller transverse diameter than in the Miocene genus; the anterior half of the crown is much less concave on the inner side, and it would seem that the internal tubercle was rudimentary and the posterior valley small. At all events, the greater simplicity of the tooth can be seen from the anterior half of the crown, which is uninjured.

The true molars differ in several important respects from those of *Oreodon* and are more like, but not identical with, those of *Agriochœrus*. The inner crescents are more conical and less compressed than in the former genus, and the outer cusps are less distinctly crescent-shaped; they are also more widely separated from the inner crescents, so that the valleys are much broader and shallower. The anterior pair of crescents is much more completely separated from the posterior than in *Oreodon*, by a depression which runs across the crown. All this is equivalent to saying that in *Protoreodon* the selenodont pattern of the lower molars is much less completely developed than in *Oreodon*. Compared with the molars of *Agriochœrus*, those of the Uinta genus present the following differences : The internal crescents are convex on the inner side, instead of being concave with a median ridge, and the basal tubercles on these crescents are smaller; the outer crescents are less flattened and the bones slightly more prominent, though leaving the valleys open in front. As in this genus, the heel of the last molar is proportionately larger than in *Oreodon*.

The *brain of Protoreodon* (Pl. III, Fig. 1ᵇ), as indicated by the shape and size of the brain case, is very narrow and considerably elongated; the hemispheres are especially small and more simply convoluted than in *Oreodon* ; the convolutions are, as in this genus, rather broad and have a nearly straight fore and aft direction, converging in front; the medilateral gyrus is not very distinctly marked. The posterior region of the brain including the cerebellum and medulla is very long in proportion to the hemispheres, and apparently the *corpora quadrigemina* were partially uncovered by the interspace separating the hemispheres from the cerebellum. As a whole, the brain is distinctly smaller in proportion than in the Miocene genera of the group.

The *vertebral column* is represented in the collection by many specimens from all the regions; but as they are not in an especially good state of preservation, and as they do not show any very striking differences from the vertebræ of *Oreodon*, they will not require an extended description.

The atlas is very similar to that of *Oreodon* and resembles therefore that of the tragulines rather than that of the Pecora ; it is short in the antero-posterior direction,

but with widely extended transverse processes, which are perforated by the vertebrar-
terial canal. The anterior cotylus for the occipital condyles is quite shallow, the
posterior faces for the axis are quite flat and with greater vertical than transverse
diameter. The axis is likewise similar to that of *Oreodon*, though with differences.
The atlanteal faces are narrower than in that genus, but higher, and form a consider-
able part of the side walls of the neural canal; the odontoid process is narrower and
more peg-shaped, and the articular surface on its lower side is not continuous with
the facets for the atlas, but separated by a faint ridge; the upper surface of the pro-
cess is marked by a quite high and strong ridge, which loses itself posteriorly in the
floor of the neural canal. In *Oreodon* the upper surface of the odontoid is either flat
or, as is the case in many specimens, it shows an approximation to the spout-like
form of the ruminants in the elevation of the edges, so that it becomes somewhat
concave from side to side. The shape of the process is thus seen to be quite different
in *Protoreodon*. The centrum of the axis is keeled and quite strongly opisthocœlus;
neither neural spine nor transverse process is preserved in any of the specimens.

The other cervical vertebræ are rather longer in proportion than those of *Oreodon*
and have somewhat more markedly opisthocœlous centra; the anterior ones at least
have either obsolete or very low spines, and apparently all except the seventh exhibit
the vertebrarterial canal.

Except for their light and slender construction, neither the dorsal nor the lumbar
vertebræ present any special peculiarities; the posterior dorsals are long and com-
pressed, the lumbars become broad and depressed in the hinder part of the region.
The artiodactyl characteristic of cylindrical and interlocking zygapophyses in the
posterior dorsal and lumbar vertebræ is quite as well developed as in the White
River genera of the group. Several caudal vertebræ indicate that the animal pos-
sessed an unusually long and stout tail, even more so than in *Oreodon*, as is made
probable by the size of the transverse process upon the more anterior vertebræ.

Of the *scapula* only the distal portion is preserved, which is, however, sufficient
to show its more essential characters. The glenoid cavity is subcircular in outline,
much as in *Oreodon* and Hyopotamus; the coracoid process is recurved and promi-
nent, and the spine rises abruptly from the neck, as in *Oreodon* and the ruminants,
and having a very different shape from that which occurs in the pigs. As far as can
be judged from the fractured condition of the specimens, the spine may be said to
divide the blade into nearly equal pre- and postscapular fossæ. This position of the
spine is rendered the more probable from the fact that it occurs in *Oreodon* and
Hyopotamus, with the scapula of which the portions of the shoulder blade of *Pro-
toreodon* which are preserved in the collection closely agree.

The *humerus* agrees closely with that of *Oreodon*, which, as Cope has pointed out (No. 4, p. 508), is very peculiar and differing from that of all recent artiodactyls, finds its nearest analogue in *Anoplotherium.* "The greater tuberosity is large, rising above the head; and is incurved, terminating inwards in an acuminate apex. Its border at the base is thrown into an obtuse angle. The lesser tuberosity is small, and is well separated from the greater by a deep and wide bicipital groove. The deltoid ridge is distinct. The condylar extremity is more transversely extended than in any recent artiodactyl, owing to the fact that the posterior internal distal tuberosity is placed interior to the trochlea instead of partially behind it, and that there is, in addition, an internal epicondyle not seen in the recent suilline or ruminant members of the order. The intercondylar ridge is strong, and wider than in most recent ruminants; in the suillines it has nothing like such a development. Another peculiarity is the flange-like free border of the external trochlea, which is especially recurved at its superior part." With a few modifications this description will apply equally well to the humerus of *Protoreodon.* The shaft is rather more slender and the deltoid ridge much less massive and prominent; the anconeal fossa is narrow and very deep, perforating the shaft, as is also generally the case in the Miocene genus.

The *ulna,* as would naturally be expected, shows no tendency to coössify with the radius; the olecranon is unusually long and stout and deeply grooved at its upper end; the sigmoid notch forms somewhat less than a semicircle and passes below into two small facets for the head of the radius. The shaft is stout and trihedral in the upper portion, but becomes very much compressed below and presents a deep groove on the internal side. The distal end is not preserved in any of the specimens. This bone shows more differences from the corresponding element of *Oreodon* than does the humerus; the most important of these are the proportionately greater size of the olecranon and the singular flattening and grooving of the shaft.

The *radius* differs but slightly from that of *Oreodon,* as far as the fragments preserved allow of comparison. The surface for articulation with the humerus is a rather broad head, which is much compressed from before backwards; the articular facets form three portions, a median concavity for the intercondylar ridge, or tuberosity it might be called, and a more flattened surface on each side of this. The external beveled surface for the curious flange on the humeral condyle above mentioned, is more concave and descends lower on the anterior face of the bone than in *Oreodon,* and the anterior edge is somewhat more sinuous than in that genus, though there is no emargination for the intercondylar ridge, such as occurs in the anterior proximal edge of the radius in the recent ruminants, and, in a much less marked degree, in the suillines. This structure of the head of the radius is highly charac-

teristic of the *Oreodontidæ* and is correlated with the equally characteristic shape of the trochlea of the humerus. The ulnar facet on the posterior side of the head of the radius is much less conspicuous than in *Oreodon*. The shaft has a somewhat flattened, transversely oval shape, which does not tend to become cylindrical, as is the case in *Oreodon*. Unfortunately we have not been able to identify the distal end of the radius.

The *carpus.* As one would naturally expect, the structure of the carpus of *Protoreodon* is very much like that of the Miocene members of the family, though some variations of importance may be observed, especially that the various elements are less cuboidal in outline and of lighter construction.

The scaphoid is more extended transversely and less antero-posteriorly than in *Oreodon;* the proximal surface is more deeply concave, the rising in front more abrupt and the radial facet descends further on the anterior side; on the distal surface the facet for the trapezium is distinctly larger than in the Miocene type, where it is exceedingly minute; the trapezoid facet is also larger in proportion, while that for the magnum is correspondingly smaller, nor are there any such anterior ridge and posterior concavity as are to be seen in the later representatives of the family. In *Oreodon* the lunar, as Cope has pointed out, has the remarkable peculiarity of resting almost entirely upon the unciform, while the magnum has moved almost completely under the scaphoid, a tendency which reaches its maximum in *Merycochœrus* and *Merychyus*, when there is only a lateral contact between the lunar and the magnum. Among recent artiodactyls, the only group where such a displacement of the carpal elements is to be found is that of the Tragulina.

In *Protoreodon* the same peculiar construction of the carpus appears, but it has not been carried to quite the same extent. The lunar has a greater antero-posterior diameter, the radial surface is more extended in the same direction and is not nearly so strongly convex. The distal beak-shaped prolongation, which passes between the magnum and the unciform, has not moved quite so far toward the radial side, and even in front the lunar rests somewhat, though but slightly, upon the magnum, while, behind, the magnum is proportionately much larger and presents more directly downwards, instead of being rather more lateral than distal, as is found to be the case in *Oreodon*. The unciform facet of the lunar is of course smaller than in the last-named form. The Uinta genus thus presents a transitional stage between the carpus of the more typical artiodactyls and that characteristic of the *Oreodontidæ*, though the tendency towards the latter is already very distinct.

The cuneiform differs more from the corresponding bone in *Oreodon* than does any of the other carpal elements. Indeed, the specimen which we have regarded as

the cuneiform of *Protoreodon* may possibly belong to some other genus, though this is not at all probable from the association in which it was found. It is much more extended transversely and less antero-posteriorly than in *Oreodon*, as is also the scaphoid ; the ulnar facet is a simple groove which does not descend upon the outer side of the bone, thus agreeing with *Oreodon* and differing very markedly from *Dicotyles ;* the pisiform facet is very large, nearly flat, and occupies the entire posterior surface; the unciform facet is likewise quite different from that of *Oreodon* in being shallow, of less antero-posterior and greater transverse extent. In general the cuneiform of *Protoreodon* is quite low and broad, with an *f*-shaped upper contour, highest on the internal or radial side and sloping down towards the external side. Neither trapezium nor trapezoid is represented in any of the specimens, but judging from the facets on the scaphoid, both of these bones were better developed than in *Oreodon*, implying a larger relative size of the lateral digits.

The magnum, on the contrary, is smaller and of a somewhat different shape ; the proximal surface is divided nearly evenly between the facets for the scaphoid and lunar which meet at a high angle so as to form a sharp ridge along the superior median line. Seen from the side the upper contour of the magnum forms a flattened arch, whereas in *Oreodon* the magnum is quite low in front and rises abruptly behind, and nearly the whole of the proximal surface is taken up by the facet for the scaphoid. Another difference consists in the long hook-like process which in *Protoreodon* is given off from the posterior surface of the bone, and which in *Oreodon* is represented by a mere rudiment. When the bone is in its natural position the distal surface for mc. III presents obliquely downwards and outwards, even more obliquely than in *Oreodon*. As usual in unreduced artiodactyls there is a small facet on the radial side of the magnum for mc. II.

The unciform likewise presents some important differences from that of *Oreodon*. In this genus the lunar and cuneiform facets are of very nearly equal size, while in *Protoreodon* the latter considerably exceeds the former, as naturally follows from the already-mentioned fact that the lunar rests less completely on the unciform than in *Oreodon*. The surface for the attachment of the cuneiform is less distinctly convex and extends more closely to the external side of the bone than in the Miocene forms. On the distal surface the facet for mc. IV is smaller and that for mc. V larger than in *Oreodon*, and the latter is more distal in position and less crowded to the external side by the increased development of mc. IV than in *Oreodon*. This difference brings about a further one in the shape of the inferior contour, which is more regularly curved from side to side and not so distinctly angulated in *Protoreodon*. The lateral facet for mc. III is of about the same proportions.

The *metacarpals* are but scantily represented in the collection, and only one of these exhibits the proximal end. Fortunately, however, this is the first metacarpal or pollex, the existence of which would naturally be inferred from its presence in *Oreodon*. There can no longer be any question as to the pentadactyl character of the fore foot in *Oreodon*, as two specimens of *O. Culbertsoni*, Colorado and Dakota, with the pollex in position, are preserved in the Princeton Museum, and in the Museum of Comparative Zoölogy there is a beautifully preserved manus of *O. gracilis* in which all five digits lie in their natural position in the matrix. In *Protoreodon* the first metacarpal is proportionately better developed, being both stouter and longer, than in *Oreodon*. Its proximal end has a nearly flat head for articulation with the trapezium. In none of the specimens of *Oreodon* mentioned have any phalanges been found in connection with mc. i, though the distal end is rounded and faintly keeled on the palmar side, indicating the probable existence of phalanges. Such were certainly present in *Protoreodon*, as is shown by a small proximal phalanx belonging to the pollex. Its proximal facet is very oblique, sloping strongly outwards, and is but slightly concave. Its distal surface plainly shows the articulation for the ungual. The pollex, though of small size, was thus present in all its parts, and the importance of this fact as connecting the artiodactyls with the always pentadactyl Condylarthra is obvious. It seems almost certain that artiodactyls with unreduced anterior feet existed through the Bridger and Wasatch periods, though it is somewhat surprising to find them persisting so late as the White River Miocene.

The *pelvis* is not well preserved in any of the specimens. Several fragments seem to show that in construction it is essentially like that of *Oreodon*, and therefore rather suilline in character. The ilium has a long compressed peduncle which expands rather abruptly into a large terminal plate for articulation with the sacrum. There is no supra-acetabular fossa. The length of the ischium could not be ascertained.

The *femur* would seem to be longer and stouter proportionately than in *Oreodon*. The rotular trochlea is very prominent and quite narrow, and has the inner edge higher than the outer. A difference from *Oreodon* is shown in the presence of a fossa for the plantaris muscle instead of a rugose surface, though, as Kowalevsky has shown, no great importance can be attached to this character.

The *tibia* is only imperfectly represented; some points may, however, be made out with regard to it. It is entirely unankylosed with any portion of the fibula, and has a stout shaft of transversely oval section below, above it is more trihedral. The distal end is very like that of *Oreodon*, with deeply incised grooves for the astragalus and a very well-developed malleolar process.

The *fibula* is entire but very slender. Its distal end is closely applied to the

astragalus, forming a large external malleolus, and as in all artiodactyls rests upon the fibular facet of the calcaneum.

The *hind foot* is very closely similar to that of *Oreodon*, even more so than is the fore foot. The astragalus is somewhat narrower in proportion to its height and the difference between the external and internal condyles in size is somewhat more marked. The internal condyle passes directly into the navicular facet, though interrupted by a slight prominence. The distal end is very unequally divided between the navicular and cuboidal facets, the former being much the larger; the difference is perhaps even more marked than in *Oreodon*. These two genera agree thus with *Anoplotherium* and the Suina and differ from most ruminants in which the two facets are of more nearly equal extent. The calcaneal facets and those for the malleolar processes of the tibia and fibula resemble the corresponding parts in *Oreodon*, except that the distal calcaneal surface is larger. The calcaneum is much more slender than in *Oreodon* and is especially less expanded at the distal end. The fibular facet rises to a greater height and distally is more abruptly marked, and the interval between this facet and the distal end is considerably greater than in *Oreodon*. The sustentaculum projects further internally, though decidedly small, as in all oreodonts. The cuboidal facet is more arched and concave from before backwards, and narrower from side to side, while the distal astragalar surface is flatter and larger. In fact, the calcaneum differs from that of *Oreodon* more than does any other tarsal bone.

The cuboid is higher and narrower than in *Oreodon* and the astragalar and calcaneal facets more equal, though the latter is somewhat broader. In correspondence with the greater length of this part of the calcaneum, the cuboid is much more deeply incised by the calcaneal facet, and the anterior edge of the navicular surface rises high above it. The distal surface of the cuboid displays the usual facets for the fourth and fifth metatarsals; the latter is larger and the former is smaller than in *Oreodon* and of somewhat different shape. Another difference from this genus consists in the greater extension of the hook-like projection from the rear of the cuboid. In fact the differences are so striking as to raise the suspicion that the specimen described belonged to some other genus, as unfortunately it was not associated with teeth. But from its correspondence with the calcaneum it very probably should be referred to *Protoreodon*, and its differences from the cuboid of ruminants and pigs are even more marked than from *Oreodon*.

The navicular is likewise higher and narrower than that of *Oreodon*, but otherwise resembles it very closely; its proximal surface is somewhat more deeply concave and its anterior edge rather more sinuous. Cope's statements (No. 4, p. 510) with regard to the cuneiforms of *Oreodon*, are in some respects inaccurate, and

require correction before we proceed to the comparison with *Protoreodon*. Cope's description is as follows: "The ectocuneiform is distinct, and much wider than long. The mesocuneiform is extero-posterior in position, and the transverse diameters are small. It is produced distally overlapping the head of the second metatarsus. Entocuneiform wanting." In reality the ecto- and mesocuneiforms are coössified, the line of junction between them being marked by a slight step, or difference of level on the distal surface, which indicates the two facets for the second and third metatarsals respectively, and what Prof. Cope has called the mesocuneiform is really the entocuneiform. If Prof. Cope's statements were correct, *Oreodon* would present the remarkable anomaly of having the ectocuneiform support two digits, while the mesocuneiform supports none at all, or in other words, having the second metatarsal shifted outwards from its ordinary attachment. Besides this, the ectocuneiform persists with remarkable constancy in the ungulate series, and its absence in such an unreduced pes as that of *Oreodon* would be very extraordinary. But as we have seen, these anomalies do not exist. In *Protoreodon* almost exactly the same conditions are found as in the Miocene genus, only here the difference in height between the meso- and ectocuneiforms and consequently the distal step is more pronounced. The entocuneiform is not preserved in any of the specimens, but the facets on the navicular and second metatarsal show that it was shaped very much as in *Oreodon*.

The *metatarsals* are four in number and entirely free; no trace of the hallux has been found, and in all probability none existed. The metatarsals are of more equal development than in *Oreodon*, the lateral ones being somewhat larger in proportion to the median, as would be inferred from the structure of the distal row of tarsals; in other respects they are closely alike. The second metatarsal has a somewhat lateral bearing on the ectocuneiform, and metatarsals III and IV are closely interlocking. The ridge on the distal end of the metapodials is confined to the palmar surface.

The *phalanges* also resemble those of *Oreodon*, those of the first row being long and depressed, those of the second row shorter and with the distal trochlea even less asymmetrical than that of *Oreodon*, showing a less degree of convergence of the hoofs than in that genus, and hence very much less than in any of the recent artiodactyls except the Tylopoda. The ungual phalanges are, as would be inferred from this, but slightly asymmetrical; they are higher, narrower, more pointed, and altogether more claw-like than in the Miocene members of the group, with the exception perhaps of *Merychyus*.

The only clearly characterized species of *Protoreodon* is *P. parvus* S. & O., of which the type specimens are the skull and lower jaws figured on Pl. I, Figs. 1 and 2. This was a very small animal, inferior in size even to *Oreodon gracilis*. The

measurements agree fairly well with those of the so-called *Agriochœrus pumilus* Marsh, with which this species may prove to be identical.

Measurements. M.

Length upper molar series (entire).. ? .053

" " premolar series.. ? .026

" " true molar " .... .027

Length lower molar series (entire) .... .054

" " premolar series.. .027

" " true molar " .... .027

Third upper molar, antero-posterior diameter.. .010

" " " transverse " .... .008

" lower " antero-posterior " .... .012

" " " transverse " .... .006

Although the teeth preserved in the Princeton collection all belong to *P. parvus*, there are several limb and foot bones which exceed those of the type species so greatly in size, that they very probably belong to a larger species. They differ, however, only in size and must unquestionably be referred to the same genus. Size alone is not a very satisfactory criterion, but it seems unlikely that such differences can be within the limits of mere sexual or individual variation. The following measurements will show the size of these larger specimens of *Protoreodon* as compared with that of *Oreodon Culbertsoni*.

Measurements.

	Protoreodon.	*O. Culbertsoni.*
	M.	M.
Breadth of humeral trochlea.............................	.016	.021
Height " " "	.011	.013
Length of calcaneum	.050	.052

Systematic Position and Relationships of Protoreodon.

It will be obvious from the foregoing description that *Protoreodon* is very closely allied to the White River genus *Oreodon*, and may safely be regarded as the ancestor of that genus. This relationship is made clear by a comparison of the skull, the teeth and the feet, where the differences which *Protoreodon* exhibits from its Miocene successor are just these tendencies towards the simplification that we should naturally expect to find in the ancestral type. More particularly the presence of the fifth cusp in the upper molars is a welcome indication of the connection between the oreodonts and the buno-selenodonts of the earlier Eocene. On the other hand, *Protoreodon* has many points of resemblance to *Agriochœrus*, which are somewhat as follows: (1) The shape of the cranium and the remarkable elongation of its posterior portion; (2) the

open orbit and probable absence of the lachrymal depression; (3) the position and shape of the posterior nares; (4) the position of the infraorbital foramen; (5) the character of the anterior premolars; (6) the character of the lower molars and of the internal part of the upper. These differences of importance separate *Agriochœrus* from *Protoreodon*, namely, that in the former there are considerable diastemata in both upper and lower jaws, that the last premolar has assumed more or less completely the pattern of the molars, and that the outer crescents of the upper molars are over-hanging.

Can *Protoreodon* then be regarded as the common ancestor of both sections of the Miocene family, the *Oreodontinœ* and the *Agriochœrinœ?* As to the derivation of the former subfamily from this genus there seems to be no reasonable doubt; its relations to the second are more obscure. If we accept Schlosser's view that a closed dental series is always secondary, and a sign " dass der betreffende Stamm am End-ziel seiner Entwicklung angelangt ist, wenigstens finden wir diesen Zustand, nur bei solchen Formenreihen, welche gerade im Aussterben begriffen sind " (No. 13, p. 46), it is clear that *Agriochœrus*, with its diastemata, cannot be derived from *Protoreodon*. But even if this principle be generally true, it is not without exceptions, as the long persistence of the oreodonts themselves demonstrates, and the diastemata are, there-fore, of themselves insufficient to decide the question. A more important difficulty is the constitution of the outer crescents of the upper molars, which in the known species of *Protoreodon* have commenced to assume the flattened shape characteristic of *Oreodon*. The Uinta genus therefore stands very near to the common ancestor of *Oreodon* and *Agriochœrus*, but seems itself not to be that ancestor, at least so far as we may judge from the teeth of *P. parvus*; it is quite possible that another species of the same genus may stand in the same relation to *Agriochœrus*.

The forerunner in the Bridger fauna of *Protoreodon* would seem to be *Helohyus* Marsh, known as yet only from the teeth. In this genus the upper molars have five cusps, the unpaired one in the anterior half of the tooth, which are of a pyramidal shape, and refer the genus to the generalized group of buno-selenodonts, which is represented by the Eocene hyopotamids of Europe. If more perfect specimens shall confirm this supposed connection between *Helohyus* and *Protoreodon*, it will demon-strate the connection of the *Oreodontidœ* with the *Anthracotheridœ*, which has been already often surmised. With regard to the connection of the former group with the Tylopoda, we have seen in considering *Leptotragulus* that the relationship is proba-bly a very remote one, and that the Tylopoda seem to pass backwards into the *Dich-obunidœ*, from which Schlosser derives the typical ruminants and the Tragulina.

In his later papers (No. 5, p. 384) Prof. Cope has included *Protoreodon* among

the *Xiphodontidæ* on account of the presence of the fifth cusp in the anterior half of the upper molars. This arrangement is, however, quite untenable, as this unpaired cusp is common to the great majority of the selenodonts and even the bunodonts of the Eocene. On the other hand, the peculiar structure of the premolars in *Xiphodon*, the caniniform premolar of *Protoreodon*, and the entirely divergent structure of the feet in the two genera, show that their relationship to each other can only be a remote one, and that any association of them in a single family must be arbitrary. This is especially the case when we consider the obviously close relationship between the *Oreodontidæ* and *Protoreodon*, which is recognized in Cope's scheme (*l. c.*, p. 387). If the presence of the fifth cusp be looked upon as a family character, then it will be necessary to form a new family, the *Protoreodontidæ*, for the reception of this genus. But this seems to be unnecessary, and a more natural method would be to regard the Uinta type as forming a subfamily of the *Oreodontidæ*, characterized by the five-lobed upper molars, and in other respects combining the features of the Miocene subfamilies, the *Oreodontinæ* and the *Agriochœrinæ*. This last fact is of particular importance, as it proves the connection between *Agriochœrus* and the true oreodonts, and shows that Cope's reference (*l. c.*, p. 388) of this genus to the *Dichodontidæ*, on account of the complication of the last premolars, does not represent the natural arrangement. Whether we adopt Leidy's view, that *Agriochœrus* is the type of a distinct family, or with Gill regard it as representing a subfamily of the *Oreodontidæ*, is a matter of comparatively little importance ; the essential fact being the close genetic connection of the two.

List of Papers Quoted.

E. D. Cope.—1. On the Vertebrata of the Wind River Eocene Beds of Wyoming. Bulletin U. S. Geological and Geographical Survey of the Territories, Vol. VI, No. 1, pp. 183–202.

2. The Mesozoic and Cænozoic Realms of the Interior of North America. American Naturalist, Vol. XXI, pp. 445–462.

3. The Vertebrata of the Tertiary Formations of the West. Report of the U. S. Geological and Geographical Survey of the Territories, Vol. III, Pt. I, Washington, 1884.

4. Synopsis of the Species of Oreodontidæ. Proceedings of the American Philosophical Society, Vol. XXI, pp. 503–572.

5. The Classification and Phylogeny of the Artiodactyla. *Ibid.*, 1887, pp. 377–400.

Clarence King.—6. U. S. Geological Exploration of the Fortieth Parallel. Vol. I, Systematic Geology, Washington, 1878.

Joseph Leidy.—7. The Extinct Mammalian Fauna of Dakota and Nebraska. Journal of the Academy of Natural Sciences, Philadelphia, 1869.

O. C. Marsh.—8. Notice of New Tertiary Mammals. American Journal of Science and Arts, 3d Ser., Vol. IX, pp. 239–250.

9. Introduction and Succession of Vertebrate Life in America. *Ibid.*, Vol. XIV, p. 337.

H. F. Osborn.—10. A Memoir upon *Loxolophodon* and *Uintatherium.* Contributions from the E. M. Museum of Geology of the College of New Jersey, Princeton, 1881.

L. Rütimeyer.—11. Beiträge zu einer natürlichen Geschichte der Hirsche. Abhandlungen der Schweizerschen Palæontologischen Gesellschaft, Vols. VII, VIII and X (separatim).

Orestes St. John.—12. Report on the Geology of the Wind River District. Twelfth Annual Report of the U. S. Geological and Geographical Survey of the Territories for the year 1878, pp. 175–269.

M. Schlosser.—13. Beiträge zur Kenntnis der Stammesgeschichte der Hufthiere, etc. Morphologisches Jahrbuch, Bd. XII, pp. 1–236.

14. Die Nager des Europäischen Tertiärs, etc. Palæontographica, Bd. XXI, pp. 21–164.

W. B. Scott.—15. The Eocene Lacustrine Formations of the West. Proceedings of the American Association for the Advancement of Science, 1887.

16. On some New and Little Known Creodonts. Journal of the Academy of Natural Sciences of Philadelphia, Vol. IX, pp. 155–185.

W. B. Scott and H. F. Osborn.—17. Preliminary Report on the Vertebrate Fossils of the Uinta Formation. Proceedings of the American Philosophical Society, 1887, pp. 255–264.

C. A. White.—18. Report on the Geology of a Portion of Northwestern Colorado. Tenth Annual Report of the U. S. Geological and Geographical Survey of the Territories, 1876, pp. 3–60.

PART III.

BY HENRY FAIRFIELD OSBORN.

THE PERISSODACTYLA.

It is necessary to open this section with some observations upon the synonymy of the Eocene Perissodactyla. With the assistance of Prof. Marsh, the writer recently examined the types in the Yale College collection, in comparison with those at Princeton. The result shows that the entire nomenclature of these genera is in utter confusion, arising from the attempts which have been made by others to work from the brief descriptions given by Prof. Marsh and without the aid of figures. This confusion extends through all the American and foreign literature which relates to the American Eocene fauna, and invalidates a great deal of otherwise very useful work.

The synonymy of *Helaletes* (Marsh) is *Dilophodon* (Scott) and *Desmatotherium* (Scott). *Lophiodon nanus* (Marsh) also belongs to this genus. *H. latidens* (nobis) must be separated from it. It was originally distinguished from *Hyrachyus* by the presence of a third lobe on the last lower molar; this lobe is very small and forms the only distinction between the type and the mandibular dentition of *Dilophodon minusculus*. The maxillary dentition is precisely like that of *Hyrachyus*, except in point of size and in the presence of two internal lobes upon the third and fourth premolars. The latter feature was given by us as the generic distinction of *Desmatotherium*. The dental structure (excepting only the rudimental third lobe) and the tarsal characters remove it entirely from the tapir series, and relate it to *Triplopus*, from which, however, it is probably generically distinct. *Colonoceras* has precisely the dentition of *Hyrachyus agrarius* Leidy. The rudimental horn cores upon the nasals may serve as a generic distinction, although, in the very limited knowledge we have of the nasals of *Hyrachyus*, this character is not altogether satisfactory. *Limnohyus* is a *nomen nudum*, having been applied to a type already preoccupied by *Palæosyops*. Prof. Marsh will apply a new generic name to his *L. laticeps*.

The primitive horses are in much confusion. *Eohippus** (Marsh) is a synonym

* Am. Jour. Sci. and Arts, Nov., 1876, p. 401.

of *Hyracotherium* (Owen).   *Orotherium** (= *Lophiotherium*) was based upon a good type lower jaw ; it has the last lower premolar like the molars ; it is identical with and precedes *Orohippus*,† which was founded upon an uncharacteristic type (*O. pumilus*, a number of loose upper molars), and was not fully defined until later upon the discovery of *O. agilis*.   Both genera are, however, synonymous with *Pliolophus* Owen, which is defined by the last premolar being like the molars.   The species, *O. agilis*, is however founded upon a type in which the third and fourth upper premolars have two internal lobes ; it thus falls within the definition of *Epihippus*.‡   *Epihippus* is thus in turn close to *Anchilophus*, but may be distinguished from it by the more depressed crests and less complete union of the para- and metaconules into transverse crests.   Then follows *Mesohippus* with three premolars like the molars, and crests like those of *Anchilophus*.

There is a remarkable parallelism in the assumption of the molar pattern by the premolars in all the perissodactyl series.   We can almost predicate of any Wasatch genus, fourth premolar unlike the molars ; of any Bridger genus, fourth premolar like the molars ; of any Uinta genus, third and fourth premolars like the molars ; of any White River genus, second to fourth premolars like the molars.

PERISSODACTYLA.

AMYNODON.

Numerous errors have found their way into the descriptions of the skull and dentition of this genus which require correction before its affinities can be discussed. There are now three skulls known which may be referred to three species.   First, the type *Amynodon advenus* Marsh, from the Uinta beds ; second, the type of *A.* (*Orthocynodon*) *antiquus*, nobis, from the Washakie beds ; third, the type of *A. intermedius*, spec. nov., from the Uinta.

Prof. Marsh's description of the type is as follows :§   "The skull is intermediate in form between that of a tapir and a rhinoceros, but the molar teeth are entirely of the latter type.   The premolars are all unlike the molars, and the canines above and below are very large.   The incisors are small and the inner one in each jaw is lost in the present adult animal.   The lower canines are placed nearly horizontal, and, taken in connection with the rest of the anterior dentition, they prove conclusively that the large lower teeth usually regarded as incisors in *Aceratherium* * * * are really canines."   The number of digits is stated to be **4–3.**   This description is erroneous

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* Am. Jour. Sci. and Arts, Sept., 1872, p. 217.

† *Op. cit.*, proposed Sept., 1872 ; defined May, 1873.

‡ Introd. and Succession of Vert., etc., Aug., 1877, p. 28.

§ Am. Jour. Sci. and Arts, Third Ser., Vol. XIV, p. 251.

in most of the particulars, partly owing to the fact that it was drawn up before the type specimen had been removed from the matrix and put together, and in this way, even after examining the type ourselves, as Prof. Marsh kindly allowed us to do, we were formerly led to consider the Bridger species as a distinct genus (*Orthocynodon*).

A second examination of the type specimen recently made brings out several important diagnostic characters in addition to those already noted in our preliminary bulletin, p. 262. There are three lower and probably three upper incisors; the first lower premolar is wanting. The canines are erect. There are rugose postorbital, antorbital and infraorbital processes. The nasals are very short and slightly over-hang the anterior nares. The type of *A. antiquus* is still found to resemble that of *A. advenus* closely, with the important exception that there are four lower premolars instead of three, the first lower premolar being fully functional and bifanged; the first upper premolar is missing. It may subsequently be found to represent a distinct genus as we at first supposed, for which the original name *Orthocynodon* would stand. The *A. intermedius*, besides its much larger size, may be clearly distinguished from the two foregoing by the procumbent position of the canines and by the retention of a single fanged first upper premolar.

These and other characteristics throw a new light upon the phylogenetic position of the *Amynodontidæ*, which will be discussed later.

AMYNODONTIDÆ S. & O.*

Rhinoceros-like animals extending from the Middle Eocene to Lower Miocene; skull deeply excavated in front of orbit; incisor border very broad; nasals short and hornless; canines and incisors present and functional in both jaws; pattern of the molars like that of the rhinoceros except for the non-reduction of the external crest of the third upper molar; probably four toes in front and three behind; probably astragalus rests upon the cuboid as in the rhinoceros.

This definition is considerably modified from that previously given by the writers, in order to embrace the Miocene genus.

The genera embraced in this family are:

Lower Miocene (*White River*).

METAMYNODON,† nobis. Dentition, i. $\frac{?3}{3}$, c. $\frac{1}{1}$, pm. $\frac{3}{2}$, m. $\frac{3}{3}$. Upper and lower canines obliquely placed, the latter fitting somewhat internal to the former when the

* E. M. Museum Bulletin, No. 3, 1883, p. 4.

† Bulletin of the Museum of Comparative Zoölogy, Sept., 1887, p. 165.

jaw is closed. The second, third and fourth upper premolars of the molar pattern. Postglenoid and posttympanic processes widely united. Periotic not exposed.

Upper Eocene (Uinta).

AMYNODON* Marsh. Dentition, i. $\frac{?3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4-3}{4-3}$, m. $\frac{3}{3}$. Upper and lower canines erect or obliquely placed. The third and fourth premolars of the molar pattern. Postglenoid and posttympanic processes separated. Digits: 4–3 (Marsh).

A. ADVENUS Marsh. Premolars $\frac{3}{3}$. Number of upper incisors uncertain. Upper canines obliquely placed, lower canines erect.

A. INTERMEDIUS, spec. nov. Premolars $\frac{4}{?}$; first upper premolar rudimentary and single fanged. Canines in both jaws very large, semi-procumbent, oval in section. Three functional upper incisors.

Middle Eocene (Washakie).

A. (ORTHOCYNODON) ANTIQUUS, nobis. Premolars $\frac{?4}{4}$; first upper premolar bi-fanged. Canines in both jaws vertical, triangular in section. Number of upper and lower incisors uncertain. Mastoid portion of periotic exposed.

AMYNODON INTERMEDIUS.

PLATE X.

This species is represented by the base of the anterior portion of a skull (No. 10,309) in beautiful preservation, showing the complete characters of the teeth, the palate, the position of the orbit and the lower portion of the premaxillaries. The four canines and an upper molar of another individual are preserved. Part of the lower jaw and a premolar of a third, and the mandibular symphysis of a fourth. There are also numerous skeletal fragments, which however cannot be referred to *Amynodon* with any certainty.

Dentition (Figs. 10, 10a). The three i n c i s o r s are equidistant; the median one is slightly larger than the lateral and is placed about as far from the premaxillary suture as the lateral incisor is from the canine. The crowns are pointed, convex on the anterior and posterior faces, and slightly compressed laterally. The c a n i n e s are very powerful, with lance-shaped crowns and a decidedly flattened oval, quite unlike the trihedral crowns in *A. antiquus;* they project forward at angle of forty-five degrees, and slightly outwards; the fangs are powerful and deeply rooted beneath the first premolar. There is a considerable diastema.

* Am. Jour. Sci. and Arts, Sept., 1877, p. 251.

The first p r e m o l a r is represented merely by the fang, which is rudimentary on one side. The second premolar has a slight swelling on the outer face which anticipates the postero-external lobe; there is a single prominent internal cusp united by two low subequal ridges with the external crest; surrounding the inner lobe is the prominent cingulum which also characterizes all the succeeding molars. The third and fourth premolars are interesting as showing a mode of development of the posterior crests quite unlike that in the tapir or Equus series; there is as yet no reduplication of the internal lobe as in the latter series, but the posterior crest grows directly out from the bilobate external crest in the valley formed by the prominent cingulum and the much broader and more elevated anterior crest; these two teeth are practically similar and submolariform, except that the third premolar has a less distinct posterior lobe and crest.
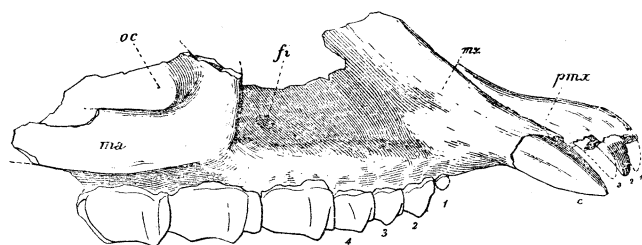
The first true molar is very similar to that in *Aceratherium;* the anterior crest has a slightly marked "anticrochet" which is entirely wanting in m.^{2} and m.^{3}; the external crest is perfectly flat and decidedly inclined inwards. The second molar has the same characters with a very decided extension of the external crest beyond the posterior transverse crest. In the third molar the external crest arches out widely beyond the posterior crest; the base of the crown is subquadrate in outline.

Measurements.

	A. antiquus.	A. intermedius.	Metamynodon planifrons.
	M.	*M.*	*M.*
Antero-posterior diameter of median lower incisor..... .011	(upper do.) .012		
Fore and aft diameter of crown of lower canine at base. .015	(upper do.) .031		.035
Upper jaw.			
Fore and aft diameter of third premolar................ .019		.021	
Length of entire molar series........................		.187	.225
" " true molar.. .... .104			.160
Fore and aft diameter first molar. .... .037		.044	.047
Transverse " " " .... .037		.043	.068
Fore and aft diameter, second molar................. .045		.053	
Transverse " " " .... .037		.052	
Fore and aft diameter, third molar................... .028		.046	.060
Transverse " " " .... .030		.046	.064
Measurement of canines, outside		.115	.130

The *skull.* The most striking features of the skull are at once seen to be the great breadth of the m a x i l l a r i e s opposite the canines and their deep excavation between the canines and the antorbital ridge; the snout is thus broader than the

anterior premolar region. The anterior nares were apparently widely open. The premaxillaries are rather narrow above and spread inferiorly, rounding and arching forwards into the broad incisive border; the relations of these bones in *Metamynodon* indicate that they had a deep area of union in front, contrasting strongly with the separate slender premaxillæ of *Aceratherium*. The m a l a r projects widely below the orbit which is immediately above the second molar and the maxillaries are deeply depressed and incurved in front of the antorbital ridge.

DIAG. 2.—*Amynodon intermedius.* Side view of the anterior portion of the skull. × ¼.

The upper and posterior regions of the skull are entirely wanting in this specimen, and have been fully described in the E. M. Museum Bulletin upon the skull of *A.* (*Orthocynodon*) *antiquus*.

The Relations of the Amynodontidæ.

The Washakie species, both in structure and time, is the most primitive form, as indicated by the complete dentition and the perfectly erect position of the canines. Then follows the *A. advenus* from the Uinta with small erect canines and the reduction of one premolar, otherwise very similar in size and dentition to the foregoing. The *A. intermedius*, while retaining the rudiments of the first premolar, which were probably lost in fully adult specimens, shows a very decided transition towards *Metamynodon* in the enlargement, shape and procumbent position of the canines, also in the broadening of the snout and compression of the antorbital region. It is singular to note how little progress the premolars of *Metamynodon* show; the second premolar is like the third, but in none are the posterior crests very prominent.

Phylogenetic Position of Amynodon.

The discovery of *Amynodon*, with its full complement of teeth and markedly rhinocerotic molar pattern, naturally led Prof. Marsh to suppose he had found the long-sought Eocene representative of the true rhinoceroses.* This opinion has been adopted by every one. But the discovery of *Metamynodon*, which is certainly far from the rhinoceros line and is an undoubted successor to these Eocene forms, directs attention to a number of developmental features which suggest an entirely distinct supposi-

* Introduction and Succession of Vertebrate Life in America, p. 30.

tion, viz., that this is another line of pseudo-rhinoceroses parallel to the *Hyracodon-tidœ*. For while the molar dentition and perhaps also the lower canines point directly to *Aceratherium*, the development of the other teeth and many characters of the skull are very diverse. Prof. Cope* presents a third alternative in deriving *Hyracodon* from *Amynodon*, placing these genera in one family, and not placing the latter in the *Aceratherium* (*Cœnopus*) series at all.

The features which unite the known *Amynodontidœ* with the aceratherine line are: (1) The structure of the lower molars and of the superior molars to the second molar inclusive; (2) the structure of the astragalus, in extending upon the cuboid. The distinguishing features of the *Amynodontidœ* are: (1) The retention of fully functional incisors in both jaws, and the great enlargement of the canines; (2) the retention of the lophiodont character of the last upper molar in its subquadrate form and complete external crest; (3) the retarded development of the posterior crests of the superior premolars; (4) the deep excavation of the maxillaries in front of the orbit and flattening of the cranium, together with the shortening of the nasals.

In *Aceratherium*, on the other hand, from the lowest American Miocene, we find the upper canines entirely wanting, also one of the incisors; the premaxillaries are narrow and weak, and support two subequal incisors. In the lower jaw are the large lateral teeth and small median pair, of very doubtful homology. Upon the discovery of *Amynodon*, Prof. Marsh suggested that the outermost lower tooth of *Aceratherium* was a canine, instead of an incisor as previously supposed, but there is little additional basis for this opinion. *A. occidentale* has, moreover, long nasals and convex maxillaries. In fact, excepting in the molar series we find no support for the supposition that *Aceratherium* is a descendant of any known species of *Amynodon*. The resemblance of *Hyracodon* to *Hyrachyus*, of *Mesohippus* to *Hyracotherium*, of *Titanotherium* to *Palæosyops* is altogether of a different character, and in each case is relatively far more significant of direct descent.

So far as Prof. Cope's suggestion of the descent of *Hyracodon* from *Amynodon* is concerned, the following objections may be made: (1) The dentition and osteology of *Hyrachyus* fill in every respect the conditions which we should expect to find in an ancestral form of *Hyracodon*, both in the displacement and reduction of the foot bones and characters of the teeth; (2) a wide difference between the aceratherine and hyracodon series is found in the structure of the carpus and tarsus. The position of the *Amynodontidœ* it appears turns upon these parts. An astragalus found near the skull of *A. antiquus* (see Diag. 12) resembles closely that of *Aceratherium* in its broad cuboidal facet. If, in addition, as we think highly probable, *Amynodon*

* The Perissodactyla. Am. Nat., 1887, p. 999.

is found to possess four toes in the manus, the series can be readily placed interme-diate between *Hyracodon* and the rhinoceroses; (3) these genera have in common a complete incisor series, but in contrast with *Amynodon*, *Hyracodon* shows a decided degeneration of the canines; (4) the molars of *Hyracodon*, while imitating those of the rhinoceros, entirely lack the peculiar proportions and inclinations of the external and transverse crests, which are so distinctly rhinocerotic in *Amynodon*.

The difficulties which have been indicated in any attempt to derive the rhinoceros from any known species of *Amynodon* do not preclude this derivation from some member of the *Amynodontidæ;* the point insisted upon here is, that such a member has not yet been discovered; secondly, that the later *Amynodontidæ* represent a dis-tinct line of pseudo-rhinoceroses, probably intermediate between the true line and the *Hyracodon* series. They approach the true rhinoceros in part of their tooth structure and probably in the foot structure, and the latter series in the remainder of the den-tal structure.

DIPLACODON Marsh.

As observed by Marsh at the time this genus was established,[*] *Diplacodon* is intermediate between the Bridger genus *Palæosyops* and the Lower Miocene *Titano-theriidæ*. Nothing is known of the skull, the type consisting merely of the palate and complete maxillary dental series. Unlike the Bridger genera the fourth premo-lar is like the molars and the second and third premolars are developing the second internal cusp, and in process of assuming the molar pattern. We may anticipate that the skull will show the initial development of the great horns of *Titanotherium*. The numerous remains of the skeleton in the Princeton collection enable us to fully confirm the relationship suggested by Marsh. The skeleton is in every detail inter-mediate between that of *Palæosyops* and *Titanotherium*, and presents a remarkable intermingling of characters persisting from its smaller Bridger progenitors and antici-pating its great Miocene successor. Allowing for a moderate elongation of the dor-sal spines, *Diplacodon* stood about five feet seven inches at the shoulder, while *Palæ-osyops* stood a little less than four feet, and *Titanotherium* considerably over seven feet. The metapodials retained the stilted spreading character seen in *Palæosyops;* much longer than in this genus and less bulky than in *Titanotherium*. On the other hand the cervical vertebræ in some species are much flattened, indicating a short neck similar to that in the Miocene genus. The detailed comparative measurements given below are taken from a *Palæosyops* species of the middle size, probably *P. palu-dosus;* the measurements of *Diplacodon* are mostly from a skeleton belonging to a

[*] Am. Jour. Sci. and Arts, March, 1875, p. 246.

single individual; the *Titanotherium* measurements are approximate from specimens which we have referred to *T. proutii*.

It is remarkable that the comparatively small genus *Palæosyops* anticipates in so many features the gigantic Miocene genus. The foot structure in almost every detail is persistent, this being the only line of Perissodactyla known in which there is no reduction of the fifth digit. Then we find in *Palæosyops*, as shown in the diagrams, every tarsal articular facet reproduced in the later genus. The neck, in some species at least,* undergoes considerable change in proportion, but the dorsal spines of the Eocene genus are decidedly elongate and anticipate the great hump of *Titanotherium*. The skull undergoes an entire remodeling, consisting principally in the elevation of the occiput, this being correlated with the elongation of the dorsal vertebral spines and development of a powerful *ligamentum nuchæ* to support the nasal horns. The earlier species of *Titanotherium*, *T.* (Megaceratops) *coloradense*, for example, retain the long nasals overhanging the premaxillaries which are so characteristic of *Palæosyops*. A feature common to the three genera is the prominence of the lesser trochanter.

In addition to the features already mentioned as distinguishing the Miocene and Uinta genera from their Eocene ally, we notice the prominent and recurved deltoid hook of the humerus; the eversion of the major axes of the innominate bones, with the marked expansion of the suprailiac border. In the manus and pes, while the facets remain the same, the proportions of the different elements are much altered, as pointed out in a later section. In the pelvis and tarsus, however, as already stated, *Diplacodon* stands nearer the older than the more recent form.

In the Washakie beds is found a large species, about the same size as *P. vallidens* Cope, which is provisionally referred to *Palæosyops* (*P. hyognathus*, spec. nov., Princeton collection, No. 10,273). This is represented by a lower jaw seven-eighths as large as the type mandible of *Diplacodon*. As in the latter, the incisors form a close procumbent series; the tips forming a gently arched line when seen from above. The symphysis is extremely long (11 cm.) and shallow; the canines are rather small and semi-procumbent. The molar-premolar series measures 24.5 cm., the last molar measures 6.5 cm., the transverse measurement outside of the canines is 9.6 cm.; in *Diplacodon elatus* the same measurement is 10 cm. Unfortunately the premolar crowns are broken; it is probable that one or two of the premolars will be found to be like the molars. The characters of the chin and symphysis are significant of close relationship to *Diplacodon elatus*.

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* In Prof. Marsh's collection there are some cervical vertebræ referred to *Diplacodon* which have about the same proportional length as in *Palæosyops*.

It is not possible to determine the species to which our skeletal remains of *Diplacodon* belong, as we have but a portion of a single upper molar. They may be referred to *D. elatus.* *Palæosyops* has hitherto been referred to the *Chalicotheriidæ*, but the discovery of the foot bones of *Chalicotherium* by Filhol shows that the genera are widely separated. The discovery of the skeleton of *Diplacodon*, however, links *Palæosyops* very closely to *Titanotherium*, and the differences between these three genera are principally in three characters, viz., the assumption of the molar pattern by the premolars, the development of frontal horns, and the loss of the incisor teeth. If these characters are given a family rank we cannot decide where to place *Diplacodon*. It seems best to group the three genera in the single family *Titanotheriidæ.**

DIPLACODON ELATUS.

Generic characters. D e n t i t i o n, fourth and third upper premolars like the molars. Last upper molar with single internal cone. D i g i t s 4–3.

Specific characters. Second upper premolar with a rudimentary postero-internal cusp, like the molars.

As above stated, the specific reference of these specimens is uncertain. The cervical vertebræ are much shorter than those associated with the Yale College specimens. It is probable that they represent a distinct species.

THE SKELETON.

PLATE VIII.

Cervicals. The *axis* (No. 10,396*a*), Fig. 15, has a broad spine overhanging the postzygapophysis. The laminæ are very slightly notched. The postzygapophyses are an elongate oval. The transverse processes are hooked, turning inwards at the tip and perforated at the base. The centrum presents a sharp inferior keel. The remaining cervicals and dorsals belong to a single individual (No. 10,396). The cervicals preserved are probably the 3d, 4th, 5th and 6th. The 5th is the most complete (Fig. 1); the spine is pointed, vertically placed and grooved posteriorly; the zygapophyses are very stout with the facets placed at angles of 45°; the vertical diameter of the centra is much greater than the transverse; they are quite strongly opisthocœlous; the transverse processes do not extend below the level of the centrum.

The centra of seven d o r s a l s are preserved. The one figured is between the

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* This generic and family name has been adopted by the writer because *Menodus* Pomel is found to be preoccupied by *Menodon* v. Meyer, and *Titanotherium* Leidy must supersede it.

7th and 10th (Fig. 2). The centrum is opisthocœlous and considerably excavated at the sides; the antero-posterior and transverse diameters are about the same; the lower half of the spine is preserved, it is a stout triangle in section indicating a great length and strongly oblique inclination; the zygapophyses are almost horizontal. One of the l u m b a r centra preserved is considerably longer than the above-described dorsal, and has a stout keel; the spine is broad (Fig. 4) and grooved posteriorly; the zygapophyses are rounded and vertically placed.

These vertebral characters closely repeat those observed in *Palœosyops*, except that the cervical centra, while nearly double in height and breadth, are only a trifle longer. In *Titanotherium* the cervicals are not further shortened, but retain the proportions seen in *Diplacodon;* they are, if anything, somewhat longer. The dorsal spines are still more elongate, forming a great hump which was incipient in *Palœosyops* and probably well developed in *Diplacodon.*

Two *ribs* are preserved which belong respectively in the anterior and middle region of the chest. They are much lighter and more rounded than in *Titanotherium.* The complete rib from the midregion has a subquadrate section in the upper third of the shaft, and an oval section in the lower third; it does not show the extreme flattened oval seen in *Titanotherium;* the length, not allowing for curvature, is 71 cm., showing that the depth of the chest was about thirty inches.

PLATE IX.

Scapula (Fig. 12). Both scapulæ are preserved, but the superior and lateral borders are incomplete. The coracoid process is a stout tuberosity. The glenoid fossa is an elongate and rather shallow oval. The spine ascends very gradually from the neck and passes without an acromial process into a deep recurved ridge; in a midsection the spine is much expanded along the border and overhangs the post-scapular fossa. The parts preserved indicate that the scapula was lofty, with a rounded suprascapular border unlike the somewhat angular border of *Titanotherium* and without any distinct indentations such as are seen in *Rhinoceros.*

Humerus (Figs. 11 and 11a). The humerus lacks the head, lesser tuberosity and bicipital groove. There is a stout deltoid ridge terminating in a prominent recurved hook. The shaft is twisted upon itself as in Rhinoceros, that is the major diameter passes obliquely from the outer posterior to the inner anterior side. The supinator ridge is less distinctly marked than in *Rhinoceros* and less prominent than in *Titanotherium.* The pronator ridge is also rugose but not projecting. The supratrochlear fossa is deeply excavated and the trochlear surfaces are somewhat oblique to the main axis of the shaft.

Ulna and *radius* (Fig. 13). These bones are complete, and taken together indicate a rather long and slender forearm. The proximal portion of the radius covers the entire ulna, and the shaft crosses to the ental side. The relative diameters of the distal facets are about as five to two. The u l n a has a very stout rugose olecranon; the posterior border presents a single concave curvature to the distal extremity; the midsection of the shaft is triangular with a deep groove upon the anterior face. The r a d i u s in midsection of the shaft is suboval anteriorly and flattened posteriorly; the facet for the ental condyle of the humerus has the same transverse, but much deeper antero-posterior diameter than that for the ectal.

The *Manus*. The carpus is entirely wanting. The metacarpus and a few of the phalanges are preserved. They show a high stilted tetradactyl metapodium of the "digitigrade" type, that is, with the phalanges resting entirely upon the ground. The distinctive feature of the foot is seen in the subequal size of the second and fifth digits, which brings the working median axis between the third and fourth digits instead of through the middle of the third. The carpus was thus undoubtedly of the type intermediate between *Palæosyops* and *Titanotherium* as restored in outline. The second metacarpal has proximally (Fig. 13*b*) a pear-shaped facet for the trapezoid, a magnum facet extending to its full depth; it also overlaps mc. III. The third metacarpal has a subquadrate magnum facet and triangular unciform facet, overlapping mc. IV by separate anterior and posterior facets. The fourth metacarpal has a corresponding mc. III facet; the unciform facet is fractured posteriorly. The fractured proximal portion of mc. V shows a narrow concave unciform facet and a lateral facet for mc. IV. The keels are entirely confined to the posterior surface, as shown in a distal view of mc. II (Fig. 13*a*). The measurements are as follows: L e n g t h, mc. III—18 cm., mc. V—13 cm. D e p t h o f p r o x i m a l f a c e t s, mc. III—3.5 cm., mc. III—3.3 cm. B r e a d t h o f d i s t a l f a c e t s, mc. III—4 cm., mc. V—3.4 cm., mc. II—3.4 cm.

The *pelvis* (No. 10,393). The marked characteristics of the pelvis are the great length of the *ossa-innominata* as compared with their breadth. The accompanying restoration of the pelvis, as viewed from above, shows the parts which are preserved in *Diplacodon* in comparison with the pelves of *Titanotherium* and *Palæosyops*. The i l i a do not expand immediately above the acetabula as in the Miocene genus, but there is a long and rather slender neck as in *Palæosyops*, beyond which they expand. The acetabular border presents a short sharp curvature, and is relatively much shorter than in *Palæosyops;* the ischial border (*ib.*) is much longer, with a gradual curvature. It follows that the suprailiac border apparently presented outwards more than directly upwards and forwards as in *Palæosyops* and *Titanotherium*—a result of the

unequal growth of the acetabular and ischial borders. The acetabular rim is much fractured; from its upper border a ridge (the pubic border) extends beneath the ilium, parallel with the ischial border to the sacral surface. Below the acetabulum the i s c h i u m has a triangular section; it then expands in a plane directly perpendicular to that of the ilium. There are no remains of the pubes.

DIAG. 3.   DIAG. 4.   DIAG. 5.
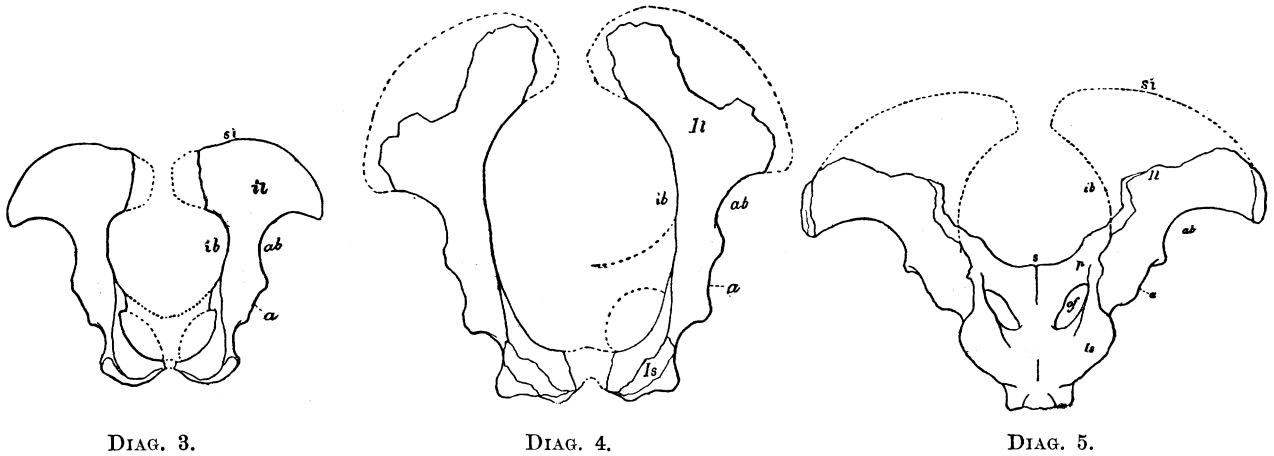
Posterior view of the pelvis of (3) *Palæosyops* × $\frac{1}{12}$, of (4) *Diplacodon* × $\frac{1}{12}$, of (5) *Titanotherium* × $\frac{1}{18}$.
Il, ilium; *Is*, ischium; *P*, pubis; *si, ib, ab*, borders of the ilium; *a*, acetabulum; *of*, obturator foramen.

The *femur*. This bone is represented by the somewhat crushed shaft (No. 10,395), and a well-preserved distal half apparently belonging to individuals of the same size, both belonging to the left side; they are combined in Fig. 5. The head and great trochanter of the former specimen are wanting. The lesser trochanter is represented by the base of a stout ridge, which indicates that it was much more prominent than in *Rhinoceros*. The third trochanter, judging by the base, was still more prominent and strongly curved forwards. It stood higher upon the shaft than in *Rhinoceros*. The lower portion of the shaft with the facets are very similar to those of the Rhinoceros, except that the patellar trochlea is longer and more deeply excavated; the condylar facets have a greater fore and aft extension, and the intercondylar notch is deeper.

Another specimen in which the head and great trochanter are preserved shows that the head was well out of the line of the shaft, with a deep pit for the round ligament. The great trochanter stands upon the level of the head.

The *tibia* (No. 10,395) is about five-sevenths the length of the femur (Fig. 6). The cnemial crest is moderately prominent. There is the usual triangular section of the shaft just below the crest passing into an oval section in the lower third. The prox-

imal and distal faces are too much worn to admit of description. Another specimen (Fig. 6a) shows a prominent internal malleolus and strong spine.

The *tarsus* (Figs. 8–8b). The well-preserved astragalus and calcaneum are of great interest. Their relations to those of *Palæosyops* and *Titanotherium* are fully discussed in the next section. The principal features of the c a l c a n e u m are the extremely narrow, deep and elongate tuber calcis, which has an unusually flattened section; there is also a distinct fibular facet, and the calcaneum also forms part of the tibial trochlea. The three astragalar facets, the ectal, sustentacular and inferior, are entirely distinct. The a s t r a g a l u s rests upon over one-third of the upper surface of the cuboid. These elements of the ankle joint indicate that *Diplacodon* was of much less bulky proportions than *Titanotherium.*

Comparative Measurements of the Skeleton, in Cm.

	Palæosyops.	Diplacodon.	Titanotherium.
(?) Fifth cervical vertebra, antero-posterior	3.2	4	6.5
" " " transverse	4.2	6.7	9
(?) Ninth dorsal vertebra, antero-posterior	3.7	6.5	6.5
" " " transverse	4.7	5.7	10
Lumbar vertebra, antero-posterior	4.7a	6	7
" " transverse	39a	6.2	10
Total length of scapula, estimated	27	60e	72a
Length of humerus	30.5	45e	67.2a
" " radius	25	35	65a
" " third metacarpal	11	18	24a
Width of carpus	6.7	10	
Depth " "	4	8e	11.2a
Total length of innominate bone	41	61	78a
Length of femur	33.5	46e	
" " tibia	27.5	33	
Width of tarsus	6.5	8.5	14.5a

a = approximate measurement.   e = estimated.

The *Palæosyops* measurements are taken from the middle size species (*P. paludosus*), which predominates in the Western Bridger basin, and while taken from different individuals are probably very nearly correct in proportion. The *Diplacodon* measurements, with the exception of the femur, tibia and tarsus, are also from portions collected together and belonging to one individual. The *Titanotherium* vertebral measurements are from a single individual, but the other parts are taken from a number of individuals. The *P. major* of the Bridger is fully one-fourth larger than the above species.

ISECTOLOPHUS S. & O.

Isectolophus is a small tapiroid, slightly larger but with shorter limbs and feet and more spreading digits than the Uinta *Triplopus.*

In the line of genera to which it belongs the characters of the premolars in respect to the gradual assumption of the molar pattern are very important. These are wanting in the Uinta specimens, but the Bridger species, which was formerly referred by us* to *Helaletes* (*H. latidens*) is closely related to *Isectolophus*, if not generically the same, and shows double internal lobes upon both pm. [3] and pm. [4]. The second upper premolar probably had two external lobes and one internal lobe. The distinctive features of the dentition, so far as known, are seen in the conic postero-external lobe of the upper molars, in the third lobe of the last lower molar and the absence of a diastema in the lower jaw. As pointed out in our preliminary description, these features place *Isectolophus* in or near the true tapir line. This conclusion is sustained by the discovery of the complete carpus and of the cuboid. The carpus is of a more primitive type than that of *Triplopus*, since the magnum and cuneiform surfaces of the lunar are subequal, as in *Hyrachyus*, while in *Triplopus* the magnum surface is much reduced, leading to the *Hyracodon* type. A still more important feature is the size of mc. v, as shown by its articular facet upon the cuneiform, indicating that there were four functional toes. The cuboid, when compared with that of *Triplopus*, is broad and reduced in vertical diameter.

Generic characters. Dentition, c. $\frac{1}{1}$, p. $\frac{4}{4}$, m. $\frac{3}{3}$. No diastema behind the canine. Fourth and probably third premolars in both jaws submolariform or with double internal lobes. Molars in both jaws resembling those of *Tapirus*. External lobes of superior molars (paracone and metacone) strongly convex and equal in size. Last lower molar with prominent third lobe. Manus and pes. Digits, 4–? 3. Lunar with subequal magnum and unciform facets. Cuboid broad with an extensive astragalar facet.

Isectolophus annectens,† nobis. The postero-external lobes of the superior molars are produced beyond the junction of the posterior transverse crests. A strong cingulum surrounds the crown.

I. (*Helaletes*) *latidens,*‡ nobis. The postero-external lobes are opposite the junction of the posterior crests. There is no cingulum.

The Bridger species may subsequently be found to represent another genus, but in the absence of the complete dentition of *Isectolophus*, it can only be separated by the characters of the molar crests, which are hardly generic. The structure of the premolars removes this genus from *Systemodon* Cope.

* E. M. Museum Bulletin, No. 1, 1873, p. 54.
† Proc. Am. Phil. Soc., Sept. 2, 1887, p. 260.
‡ E. M. Museum Bulletin, No. 1, 1878, p. 54.

ISECTOLOPHUS ANNECTENS.

PLATE X.

This genus is represented in the Princeton collection by portions of four individuals, which apparently belong to the same species, and by the type of a second species from the Bridger. The type specimen (No. 10,400) consists of the second premolar and first and second molars of the maxillary series and the last lower molar and portions of the last premolar and first molar of the mandibular series. The second specimen (No. 10,401) preserves the first upper molar and fragments of the premolars and the fourth lower premolar associated with a portion of the ramus; also a complete carpus and portions of the metacarpus; also the cuboid and metatarsal elements, in addition to the vertebral and limb fragments. The third specimen (No. 10,399) is a mandibular fragment containing the fourth premolar and first and second molars.

DENTITION.

Molars. In the type specimen (No. 10,400) m. [1] and m. [2] are preserved of the superior series. The external face is continuous but strongly trilobate (Fig. 1a) with a pronounced external cingulum and prominent anterior accessory cusp. The third lobe of m. [2] is strongly produced beyond the junction of the posterior crest (Fig. 1). The transverse crests are rather low and obtuse, curving obliquely backwards. At the head of the main valley, directly opposite the median external lobe, is a low buttress. The internal cingulum is prominent, extending upon the anterior and posterior faces of the crown. The first molar is a smaller tooth of very similar pattern.

The third lower molar (Fig. 2) has a prominent crescentic heel. The anterior crests are stout and slightly oblique; the outer face shows a crescentic prolongation inwards, which is rather faint in the middle crest but is strongly produced in the anterior crest, the crescent thus formed being strengthened by a buttress. This buttress is a marked feature of the first and second lower molars, as seen in another individual (No. 10,399). In the latter the crowns are unworn (Fig. 11), the crests are subcrescentic; the buttress is very distinct in the concavity of the anterior crest and this crest extends inwards, forming an anterior valley.

Premolars. With the type specimen there is a superior premolar (Fig. 1) in which the internal lobe is single, with a slightly paired crest extending to the outer lobes. This tooth is almost unquestionably the second premolar. Associated with the third specimen also there are portions of the external lobes probably belonging to pm. [2].

The fourth inferior premolar is preserved in each specimen (Figs. 2 and 11).

The anterior crest is lofty, bilobate, with a distinct anterior valley and buttress; the posterior crest is low, especially at the postero-internal angle. As shown in Fig. 11, the second and third premolars were bifanged, while the first premolar had a single fang and abutted closely against the canine as in *I. latidens*.

THE SKELETON.

Axial. The vertebral and other portions of the skeleton, associated with the second specimen (No. 10,401), indicate that they belong to a young individual. All the vertebral centra, lacking the epiphyses, and the contours of the posterior faces of the carpals being incompletely developed. The *vertebræ* belong to the posterior dorsal and lumbar region; the centra are much flattened vertically and slightly keeled. Fragments of the cranium and infraorbital region are present, but are not characteristic.

Appendicular. F o r e l i m b. The scapula has a suboval glenoid face, with a raised anterior border and the base of an apparently prominent coracoid process. The distance between the outer border and the rise of the spine is very narrow, indicating a rather short neck. The proximal portion of the *radius* presents a limited lateral extension, with rather deep antero-posterior diameter. These proportions, taken in connection with the rather broad carpus, indicate that *Isectolophus* had a short fore limb.

The *Carpus.* The most important portion of the skeleton is the nearly complete right c a r p u s with portions of the second and third metacarpals attached. This is the first carpus discovered belonging to any genus in this line of descent and with the *cuboid* fully establishes the systematic position of *Isectolophus* in the tapir line, as already inferred from the peculiarities of its molar teeth. The vertical diameter of the carpus proper is considerably less than the transverse, the series retaining in great measure the rather spreading character of the primitive type. The first and second rows fully alternate and interlock. The *scaphoid* has a subquadrate anterior face; the radial facet has a broad posterior extension. The trapezium facet is worn away; the trapezoid facet is excavated and is only a trifle broader than that abutting against the magnum. The *lunar* has a symmetrical radial facet with a prominent posterior hook; the inferior face presents subequal magnum and unciform facets, with closely similar angles of inclination; this is a very distinctive feature. The *cuneiform* has rather a limited transverse extension of the ulnar facet, with a small pisiform facet; the lunar and unciform surfaces are subequal. The trapezium is not preserved, but is indicated by a wide facet upon the trapezoid and upon mc. II. The

trapezoid is small, subquadrate, with convex scaphoid and metacarpal facets and sub-equal trapezium and magnum facets. The *magnum* has a pentagonal face with sub-equal scaphoid and trapezoid facets; the remaining three sides articulate—*a*, with the lunar; this facet, although narrow in front, extends back to the full depth of the lunar; also presenting a narrow unciform facet posteriorly; *b*, with the extension of mc. III; *c*, with the horizontal face of mc. III and the extension of mc. II. The *unciform* has a broad cuneiform facet, and oblique lunar facet; the inferior face presents subequal facets for the extension of mc. III and the upper face of mc. IV. The facet for the fifth metacarpal is narrow upon the anterior face and is presented obliquely outwards and backwards. The full extent of this important facet cannot be ascertained, owing to a partial fracture and the immaturity of the individual.

The *second* and *third metacarpals* have subequal shafts with a rather flattened and slender section, indicating that they were not long and that the digits were rather short and spreading. The second metacarpal has a lateral trapezium facet, a concave upper face for the trapezoid and an extension for the magnum and mc. III articulations. The third metacarpal besides the above and the deeply concave *magnum* facet has a lofty extension and abutment against the unciform. The fourth and fifth metacarpals are missing; the latter was borne upon the oblique unciform facet; the rearward extension of the unciform which forms the principal support of the toe in the tapir appears to be undeveloped. The proximal phalanges probably belonging to these metacarpals are preserved; they are elongated and rather slender.

The only portion of the *tarsus* represented is the *cuboid*, which, however, presents important diagnostic characters. It is very short and cylindroidal. The superior face is subcircular, with a large hooked calcaneal facet and a comparatively extended facet for the astragalus. The outer surface is grooved for the flexor tendons. The lower facet apparently supported mt. II and a portion of mt. III. The vertical compression of the cuboid indicates that the navicular and cuneiforms were much flattened. The distal portion of mt. III is broad with a prominent posterior keel, while mt. II is considerably narrower with an oblique face.

The distal portion of the *tibia* shows a prominent malleolus and posterior spine. The astragalar grooves are slightly oblique, and decidedly shallower than in *Epihippus*.

<div align="center"><i>Special Measurements, Skeleton.</i></div>

<div align="center"><i>Isectolophus, No. 10,401.</i>　　　　　　　　　　　　<i>M.</i></div>

Cuboid, vertical diameter	.011
" transverse "	.0095
Distal face of tibia, transverse	.014
" " " antero-posterior	.020
Carpus, vertical diameter, maximum	.019
" transverse " "	.026

Other measurements may be obtained from the plates, which are carefully drawn to scale.

Dentition, Comparative Measurements.

	Upper series, pm^1–m^3.	Upper molars m^1–m^3.	m^2 antpos-terior.	m^2 trans-verse.	Lower series, pm_1–m_3	Lower molars, m_1–m_3.	m_2 antpos-terior.	m_3 antpos-terior
Isectolophus ...... *annectens.*		.047*	.016	.018	.088*	.05*	.014*	.023
Isectolophus ...... *latidens.*		.036	.012	.013	.081	.042	.012	.018
Systemodon ...... *tapirinum.*	.063	.032	.0105	.012	.073	.035	.010	.016

The Systematic Position of Isectolophus.

Before discussing the relations of *Isectolophus*, we may review the grounds for referring this genus to a position in or near the direct tapir line: (1) As far back as the Wasatch and the overlying Wind River periods, we observe, as recently stated in full by Cope,† that a division in the lophiodont forms is indicated by the shape of the postero-external lobes of the superior molars; in one line they are conic, in the second or side line they are flattened. The former leads to the true type of tapir molar; the latter extends into another line of genera such as *Hyrachyus*, in which tapir characters were partly retained in the feet, but in which the teeth were rapidly departing from the tapir pattern; (2) another feature, to which Marsh first called attention as characteristic of this line, is the presence of a third lobe upon the lower molars; (3) a third feature is the absence of any considerable diastema behind the canine. So much for the dentition; the distinctive foot characters are more fully discussed later, they are: (4) In the carpus, the retention of subequal magnum and unciform facets upon the lunar, and the large mc. v facet upon the unciform; (5) the extension of the cuboid upon the astragalus, anteriorly and posteriorly.

The single tapiroid mark in *Helaletes* is the small third lobe of the last lower molar; in the flattened postero-external cusps, as in *Hyrachyus*, and in the high compressed tarsus resembling that of *Triplopus*, with its narrow astragalo-cuboidal contact, this genus widely departs from the tapir line. *Isectolophus*, on the other hand, has all these marks, and the points in which *I. annectens* varies from *I. latidens* are all in the direction of closer approximation to the recent tapir.

In *Systemodon* of the Wasatch (Cope Collection, see Tert. Vertebrata, Pl. LVI, Fig. 1-2), the third and fourth upper premolars have two external lobes and a

* Approximate estimate.

† The Perissodactyla. Am. Nat., 1887, p. 990.

single internal lobe.   The third has a single transverse crest, and the fourth has the second crest just developing.   In the true superior molars, the convex postero-external lobe is slightly posterior to the junction of the posterior transverse crest (metaloph), and there is a prominent cingulum embracing this lobe.   In *Isectolophus latidens* of the Bridger, which is distinguished from *Systemodon* by the double internal lobes of pm.[3] and pm.[4], the postero-external lobe is also slightly posterior to the crest, but in the Princeton specimen (*I. latidens*) there is no cingulum.   Both these forms have slight diastemata in the dental series.   In *I. annectens* the same lobe, which is homologous throughout with the primitive metacone of the tritubercular molar, is greatly produced beyond the junction of the posterior crest.   The external cingulum reappears, so that in this respect, the genus reverts to *Systemodon*, but presents such a marked advance even upon the *I. latidens* molars in other respects that it must be considered a much more recent type.   The third and fourth premolars probably show a more distinctly developed pair of internal lobes than in *I. latidens*. The inferior molars present the tapirine buttresses in the valleys and inflection of the anterior crests which are wanting in the Bridger species, but are occasionally seen in the Bridger varieties of *Hyrachyus*.   Another developmental feature is the steady growth of the anterior accessory tubercle, which is so marked in the tapir.   The comparative measurements of the teeth in these three genera show that, with the development of the molar pattern and metamorphosis in the premolars, there was a steady increase in size, extending proportionally in all parts of the dentition.

It thus appears that the primitive tapirs were well distinguished from the other lophiodonts very early in the Eocene period, and the tooth and foot structures characteristic of the recent forms were acquired even more rapidly than in the parallel line of primitive horses.

The Miocene successor of *Isectolophus* is undoubtedly represented by the single three-lobed lower molar from the White River beds, which Dr. Leidy has referred to *Lophiodon occidentalis*.   By analogy with the premolar evolution in all other perissodactyls we may anticipate that this tapir will be found to have three premolars like the molars (*Mesotapirus*).

<div align="center">TRIPLOFUS Cope.</div>

Syn. : *Prothyracodon*, nobis, Proc. Am. Phil. Soc., Sept. 2, 1887, p. 260.

This genus was discovered by Prof. Cope in the Washakie or Upper Bridger strata, and we find that it is very abundant in the overlying Uinta.   The mandibular dentition so closely resembles that of the smaller species of *Hyrachyus* described

from the Bridger, that it is possible that some of the latter belong to *Triplopus*. As Cope has pointed out, this genus is near the *Hyrachyus-Hyracodon* series, as shown by the teeth and the reduced condition of the fifth digit. It was an extremely light and graceful animal, with long slender limbs and feet of the proportions seen in *Mesohippus*, and about the height of the smaller domestic sheep. The manus and pes are extremely elongate, the podials being laterally compressed, the metapodials spreading very little, much less apparently than in either *Hyrachyus* or *Hyracodon*. The peculiarity of the manus is that the lunar rests almost entirely upon the unciform anteriorly. In the pes the cuboid is elongate and articulates with the astragalus by a very narrow joint. The genus is distinguished from *Hyrachyus* by the flattening of the external molar crests and their backward extension, also by the advanced reduction of mc. v. From *Helaletes*, by the single internal lobes of the premolars 3 and 4. There is a wide diastema behind the canine and the last lower molar is without a third lobe.

This genus is represented in our collection by portions of five or more individuals; in every case the specific determination is uncertain and the generic reference of one specimen is somewhat doubtful. The types include the *Prothyracodon intermedium* (No. 10,403) and *Hyrachyus obliquidens* (No. 10,402) of our preliminary bulletin. The former type, together with several individuals which are represented by skeletal fragments, is now referred to the same species as the latter; the latter, a superior molar, m.^{3}, evidently belongs to *Triplopus*, and has associated with it a lower jaw which either lacks or has a rudimental first premolar, a good specific distinction from *T. cubitalis* Cope. The type of *P. intermedium* cannot be distinguished from *T. cubitalis*, except by indirect association with the *T. obliquidens* type.

Generic characters. D e n t i t i o n, i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4-3}{4-3}$, m. $\frac{3}{3}$. A diastema behind the canine. Fourth and third premolars submolariform; upper third and fourth premolars with single internal lobes. External crests of superior molars flattened. Third lower molar bilobed. S k u l l, *meatus auditorius externus* closed by bone inferiorly. Tympanic expanding into a bulla. Posttympanic and paroccipital processes distinct. No postorbital arch. M a n u s and p e s. Digits 3-3. Fifth metacarpal rudimental. Lunar resting principally upon unciform. Astragalus with slight cuboidal contact.

TRIPLOPUS OBLIQUIDENS S. & O.

PLATE XI.

T. obliquidens. Syn.: *Hyrachyus obliquidens*, nobis, Proc. Am. Phil. Soc., Sept., 1887, p. 259; probably also, *Prothyracodon intermedium*, nobis, *loc. cit.*, p. 260.

Specific characters. The transverse crests of the superior molars continuous; the first inferior premolar rudimentary or wanting.

DENTITION.

The superior premolar-molar series (Fig. 6; type of *P. intermedium*, No. 10,403), consists of pm.^{3}–m.^{3}. The external crests of m.^{1} and m.^{3} are wanting, as well as the transverse crests of pm.^{3}. The external crests of the two *premolars* are subquadrate with two symmetrical vertical ridges (Fig. 6a). The anterior transverse crest of pm.^{4} is strongly recurved, forming the single internal lobe, against which the slender posterior crest abuts. The entire inner face is surrounded by a prominent cingulum. The peculiarities of the *molars* are, the elevation of the transverse crests, the concavity of the postero-external crest and faint marking of the vertical ridge. In m.^{2} and m.^{3} the external crest is produced widely beyond the posterior transverse crest, but in m.^{3} the external crest is very oblique and barely overlaps the posterior transverse crest, leaving no posterior fossa. These teeth closely resemble those of *T. cubitalis* as described by Cope,* but are slightly larger.

	Measurements.	*M.*
Superior molars (10,403).		
Third premolar to third molar inclusive		.064
Second molar, antero-posterior diameter		.015
" " transverse "		.015
Fourth premolar, antero-posterior diameter		.01
" " transverse "		.0135
Inferior molars, etc. (10,402).		
Median incisors to third molars inclusive		.102
Length of the premolar-molar series		.076
" " molar series		.042
" " postcanine diastema		.012
" " symphysis		.035
Least width of "		.016
Antero-posterior diameter third superior molar		.017
Transverse " " " "		.014

The second specimen (10,402) is the type of *T. obliquidens*. It is intermediate in size between *Hyrachyus agrarius* and *H. nanus*. There are two mandibular rami (Fig. 7) with the symphysis complete and portions of the premolar-molar crowns; also a fragment of the maxilla with m.^{1} and m.^{2} and the complete crown of m.^{3} (Fig. 10). The latter tooth resembles that of the specimen above described so closely, that it enables us to identify this specimen, first ascribed to *Hyrachyus*, as belonging to

*Tertiary Vertebrata, p. 681.

Triplopus. The fangs of three subequal incisors and a medium sized canine are preserved, behind which is an extended diastema, followed in the left jaw by the minute alveolus of pm.[1] which may have been retained *in situ* at a less mature age. In the right jaw no trace of this alveolus can be seen. If this premolar is found to be invariably missing, this may be given as the generic distinction of *Prothyracodon*. The second premolar is rather small, the third and fourth are submolariform. The three *molars* are nearly equal in size with the ordinary lophiodont pattern, the anterior crest is well incurved in the worn condition of the crown. The mandible is stout and well rounded, contracting greatly opposite the diastema. The measurements indicate a heavier jaw and larger animal than the type of *T. cubitalis*. The last molar has no trace of the third lobe, but there is a considerable space between it and the ascent of the coronoid process.

The third specimen (10,397) is of unusual interest, since it contains, associated with a few teeth, many portions of the skeleton and the complete tarsus and carpus.

The Fore and Hind Limbs.

The fore limb of *T. cubitalis* has been fully described by Cope, *op. cit.*, p. 684. It is remarkable for the unusual elongation of the fore arm and of the manus. The head of the h u m e r u s is laterally compressed, with marked fore and aft extent; the distal trochlea is unusually deep and extensive, indicating great play at the elbow joint. The distal portion of the s c a p u l a has a very long neck, and the spine rises very gradually; the scapula was probably high and narrow. The proximal facet of the radius is very deep antero-posteriorly. The u l n a is remarkable for the great extension of its olecranon; distally it is apparently more reduced than in *T. cubitalis*.

The extremities of the bones of the *hind limb* are mostly preserved, and indicate that the proportions were long and slender. The femur has a long patellar facet and a deep intercondylar pit. The tibia has a narrow but prominent cnemial crest and double spine; the distal face has a deeply excavated astragalar trochlea which is decidedly oblique. The fibula has a fairly stout distal extremity, and is throughout entirely distinct from the tibia.

The *carpus* (Fig. 6). The s c a p h o i d is very stout with a deep radial facet; inferiorly it presents a minute facet for the trapezium, an oblique trapezoid facet, subequal with the slightly larger and horizontal magnum facet. The l u n a r has a nearly horizontal unciform facet and vertical ental facet which rests partly against the scaphoid and has a slight magnum contact. The c u n e i f o r m is very thin, and has a narrow ulna facet extending into that for the pisiform. The trapezium was

extremely reduced. The trapezoid is wanting. The anterior face of the magnum is subquadrate, since the ectal lunar and unciform facets are in the same slightly oblique line. The u n c i f o r m is remarkable for its depth; superiorly it has subequal cuneiform and lunar facets; inferiorly it has subequal mc. III and IV facets and a small facet for the rudiment of mc. v. The m e t a c a r p a l s have sharp distal keels confined to the deep posterior faces. The phalanges are deep and elongate.

The *tarsus* (Fig. 9). The main features of both the carpus and tarsus are described in the section on the feet of the Perissodactyla. In addition the following features may be mentioned: The sustentaculum of the c a l c a n e u m is very narrow; the cuboidal facet slants obliquely downwards as in the Artiodactyla. The metatarsals have the proportions seen in *Mesohippus*.

Measurements may be obtained from the natural size figures upon Plate XI.

The Systematic Position of Triplopus.

Prof. Cope (Tert. Vert., p. 678; Am. Naturalist, 1887, p. 999) has placed *Triplopus* in a distinct family. He says: " The entirely rudimentary character of the fifth metacarpal, which with its digit is so well developed in *Hyrachyus*, places *Triplopus* in another family and in a distinct line of descent. I think that it must be regarded as one of the forms connecting the lophiodonts with the rhinoceroses." We cannot accept this conclusion. In the discussion of the manus and pes in the *Hyrachyus-Hyracodon* series, on a later page, it is shown that the feet of *Triplopus* are in every detail intermediate in structure between those of the above Bridger and White River genera. The teeth are also transitional. In the upper molar series of *Triplopus*, from the third premolar to the last molar inclusive, the external faces have a striking resemblance to those of *Hyracodon*, while the wearing surfaces of the same teeth are close to those of *Hyrachyus*. The departure from the *Hyrachyus* pattern is seen, first, in the decided elevation of the crests and disappearance of the posteroexternal lobe or ridge; second, in the rhinocerotic shortening of the posterior transverse crest of m. [3]; both these changes are in the direction of *Hyracodon*.

These characters suggest our considering the genus *Triplopus* as a transition form. None of the known species, however, exactly fill the requisite transition features. *T. cubitalis* and *T. obliquidens* are apparently to be considered aside from the main line, on the following grounds: The fore arm is proportionally much longer, the metapodials are more compressed, the lateral elements of the pes especially are more reduced than in any possible direct ancestor of *H. nebrascencis*. A smaller, lighter species of *Hyracodon* is, however, represented in the Harvard collection by a carpus which while slightly larger than that of *T. obliquidens* presents a very similar

stage of reduction of the lateral metapodials. This is further evidence that some species of the Lower Miocene genus will be found to approach Triplopus much more closely than *H. nebrascencis* does. The upper molars of the known species of *Triplopus* entirely lack the rhinocerotic "anticrochet" seen in *Hyracodon*, and are also devoid of the strong external cingulum.

Another feature of *Triplopus* should, however, be mentioned, which may serve to justify Prof. Cope's views of its separate systematic position, that is, the apparent expansion of the tympanic into a small auditory bulla. The *meatus auditorius externus* is completely enclosed below, whereas both in *Hyrachyus* and *Hyracodon* it is widely open.

We probably have in *Triplopus* a highly specialized cursorial type in which there is a slightly more marked tendency to monodactylism than in the predominant species of either *Hyrachyus* or *Hyracodon*. A recently completed restoration of *H. nebrascencis* from materials in the Princeton and Harvard Museums shows that the Miocene genus retained substantially the proportions of *Hyrachyus eximius* as seen in the complete skeleton discovered by Cope.

EPIHIPPUS Marsh.

This genus is represented by the lower jaw and numerous portions of the skeleton of a single young individual (No. 10,405). The species cannot be determined. The specimen is provisionally referred to *E. uintensis* Marsh.

Generic characters. Dentition, i. $\frac{3}{3}$, c. $\frac{1}{1}$, pm. $\frac{4}{4}$, m. $\frac{3}{3}$. The third and fourth upper premolars are like the molars, and the corresponding lower premolars have the double antero-internal cusps (*a a* Rütimeyer). The ulna is complete and distinct from the radius. The lunar rests equally upon the magnum and unciform. Digits 4–3.

Epihippus uintensis Marsh.

Plate XI.

Dentition. The lower jaw is shallow, tapering to the narrow, slender symphysis. The incisor fangs (Figs. 3, 3a) are equidistant and subequal. The canine is considerably larger. The first premolar has a simple pointed crown and single fang. The premolars 2–4 are missing. The second molar has the characteristic reduplication of the antero-internal cusps. From the antero-external cusp (protoconid) a sharp ridge extends downwards and inwards; there is a well-defined external cingulum. The third molar shows the same characters with a strong posterior cingulum. The superior teeth are not preserved.

Fore limb (Figs. 4, 4a). The distal portion of the humerus shows an extensive trochlea and deep anconeal pit, but no perforation. The proximal portion of the radius entirely conceals the ulna; the shaft is arched forward, strongly convex in front; the ulna descends along the flattened posterior surface and appears at the side in the lower third of the shaft. The ulna has a small pisiform and narrow unciform facet. The characteristics of the c a r p u s are fully described elsewhere and well shown in the figures. The third metacarpal does not show the increased size we should have anticipated in this genus, but would probably be relatively much larger in an adult individual. The fifth metacarpal is about three-fourths the length of the second and fourth. The phalanges are rather short and stout. The ungual phalanges spread distally. The metapodial keels are very prominent on the posterior face.

Hind limb. The t i b i a l shaft is preserved, but is not characteristic. The tarsal characters (Fig. 5) agree closely with those of *Hyracotherium*, and are fully described elsewhere. The astragalus has a very deep groove, narrow navicular facet, narrow cuboidal contact, and three distinct calcaneal facets. The calcaneum has a distinct fibula facet and rather short stout tuber; the sustentaculum is very narrow. The third metatarsal is very deep and much stouter than the second and fourth, which are strongly rotated backwards. The second metatarsal apparently articulates laterally with the ectocuneiform.

Taken altogether *Epihippus* preserves more of the primitive characteristics of *Hyracotherium* than we should have anticipated. These are especially seen in the carpus. The tarsus shows more marked reduction of the lateral members. The fibula is probably still complete.

PART IV.

BY HENRY FAIRFIELD OSBORN.

THE EVOLUTION OF THE UNGULATE FOOT.

In the Uinta and underlying Washakie beds we meet with, at least, five distinct series of Perissodactyla, representing the recent Tapiridæ and Equidæ, also the Titanotheriidæ and Hyracodontidæ, which became extinct in the Miocene, and Amynodontidæ which may have given off the true rhinoceros line. The foot bones of each of the series are fortunately represented wholly or in part in the Princeton collection and present interesting transitions to the Bridger types of feet on the one side and the White River on the other. Many notes upon the latter have been derived from the study of the collection in the Museum of Comparative Zoölogy through the courtesy of Prof. Agassiz. The writer is also greatly indebted to Prof. Cope for free access to his collection which is so rich in Lower Eocene forms.

A careful comparison of these earlier and later forms showed it to be possible to distinguish, in nearly every instance, the separate elements of the feet in each series by a number of inconspicuous but thoroughly diagnostic marks. This led the writer to a study of the minor characteristics of the foot bones in the recent and extinct Perissodactyla and the earlier Ungulata in general. Kowalevsky has given us a model for such research in his Anchitherium memoir, in which structural modification is constantly viewed from the functional standpoint, while we are greatly indebted to Cope for his numerous essays upon the broad lines and philosophy of the transitions from the taxeopod to the recent ungulate foot. The purpose of the present contribution is to indicate the chief characteristics of the foot bones in each of the phyla diverging from the primitive Taxeopoda, chiefly in their bearing upon phylogenetic questions and the laws of modification of foot structure. The subjects may be conveniently treated in the following order:

I. The foot structure in the ancestral Taxeopoda or Protungulata and the modifications which take place in the ungulates in general in the evolution from the primitive type.

II. The main features of the manus and pes in the Hyracoidea, Amblypoda, Proboscidia, Toxodontia, and in Macrauchenia.

III. The chief and minor characteristics of the manus and pes in the various series of Perissodactyla.

IV. The taxonomic value of the primitive and secondary articulations in the manus and pes.

V. The laws of modification of foot structure.

I. THE PRIMITIVE FOOT.

The more recent types are connected with the remarkably simplified feet of the Puerco ungulates by *Phenacodus;* without this link it would be presumption to describe the feet of such genera as *Periptychus, Ectoconus,* and *Meniscotherium,* as ungulate, since, excepting in the terminal phalanges, they resemble the plantigrade carnivore foot far more closely than those of any living ungulate—possibly excepting Hyrax.

The pes of the Puerco *Periptychus* and *Pantolambda* are fully known. The former corresponds so closely with that of *Ursus,* we may anticipate a similar homology in the manus, especially as the entire structure of the upper portion of the fore limb is bear-like. Our actual knowledge of the primitive taxeopod manus is at present inferential from *Phenacodus* in comparison with the more recent types in which taxeopod characteristics persist—as in most cases we can readily detect and eliminate secondary structures.

General characters. The primitive manus and pes of the lowest Eocene ungulates had five spreading digits bearing spatulate terminal phalanges marked by a median groove. The first and fifth digits were short. The separate elements of the podium and metapodium were articulated serially, the only interlocking joints being, as in all mammalia, beneath the scaphoid and unciform, cuboid and navicular. In standing, the entire sole rested upon the ground, the foot forming a right angle with the lower leg; the limited astragalo-tibial facets in all the Puerco forms leave no doubt upon this point, and we have a persistent example of this type in *Hyrax.*

THE PES. In the pes both the tibia and fibula were supported upon the astragalus; a fibulo-calcaneal facet is frequently assigned as one of the characteristics of the primitive ungulate foot,* from the fact of its appearance in so many different phyla. Among the primitive Ungulata this facet has thus far been observed only in *Meniscotherium,* it is wanting in all the other Condylarthra. (1) In this genus it has

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* See Marsh, Dinocerata, Characters of the *Protungulata,* p. 171.

a trochlear character, the fibula resting upon the calcaneum throughout extension, as in *Macrauchenia* and the Artiodactyla. (2) In the primitive Equidæ and in the Titano-theridæ, the fibula rests upon the calcaneum in extreme flexion. In ancestors of the latter family we observe this facet developing evidently as an adaptation to great body weight. (3) The third type of fibulo-calcaneal facet, as seen in the Proboscidia, (?) Dinocerata, and Toxodon,* in which the ankle motion is limited and the fibula rests broadly upon the calcaneum, is also probably a secondary adaptation to weight. As in several instances this facet has been acquired secondarily, as it is wanting in the majority of primitive taxeopods, and is not essential to the perfect working of the plantigrade ankle joint—the evidence as to its primitive character is certainly not conclusive.†

A

B.
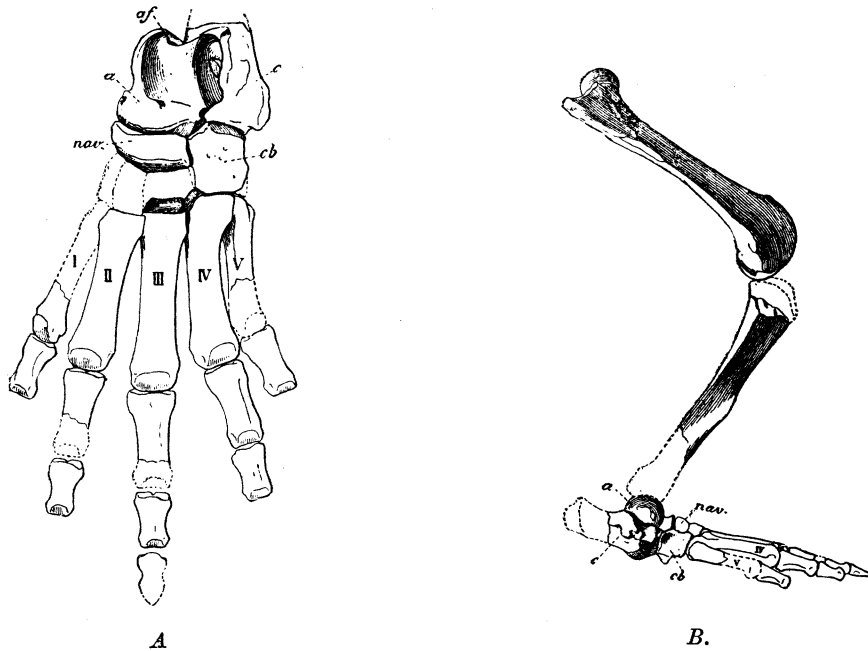
DIAGS. 6-7.—Hind limb of *Periptychus rhabdodon* Cope, from original in the Cope collection. *A*, Front view of pes, × ½; *B*, Side view of right hind limb, × ¼. The restored and conjectural portions are in dotted lines. *af*, Astrag-alar foramen.

The trochlear groove of the *astragalus* faced upwards, when the foot was prone, and with its slight concavity and obtuse edges allowed considerable lateral movement. The antero-posterior movement was evidently very limited, for this facet in all the Puerco genera is small; it was indented by a foramen probably transmitting the *flexor digitorum communis*. The importance of this a s t r a g a l a r f o r a m e n as

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* "In *Toxodon* the fibula articulation is of unusual size." Cope, Proc. Am. Phil. Soc., April, 1881, p. 402.

† We are speaking of primitive ungulates, not of primitive Mammalia in general.

a characteristic of the Ungulata and primitive Mammalia generally has been hitherto overlooked. Cope has observed it in *Bathmodon** and in *Periptychus*;† Marsh has described it as present in about one-half the *Uintatherium* astragali.‡ Lemoine§ has found it in all the Cernaysien mammals, which are of about the same age as the Puerco. It is also present in *Ectoconus, Meniscotherium, Pantolambda*, and in many if not all of the Puerco creodonts. The astragalus had a short neck articulating distally mainly with the navicular by an oval and strongly convex facet, and, while in several Puerco genera (*Periptychus, Pantolambda*), it has a considerable ecto-lateral facet for the cuboid, this facet was probably absent in the most primitive forms. Another important feature was the articulation with the calcaneum by two facets only, the e c t a l (posterior) and s u s t e n t a c u l a r (see *Phenacodus*, Diagram 10).

The *tibiale*. ‖ A careful comparison of the tarsus of *Periptychus* and *Den-drohyrax* has brought out the interesting fact that there is a broad ental facet upon the astragalus in some of the Taxopoda for the tibiale similar to that in the Hyra-coidea. This facet, which Cope has recognized as the tibiale or "internal navicu-lar" in *Periptychus*, is also observed in *Meniscotherium, Pantolambda*, and the Puerco mammals generally. It has been pointed out by Baur in *Uintatherium*, by Cope in *Bathmodon*, and should undoubtedly be added to the list of primitive characters of the pes.

The *calcaneum* resting upon the ground with its sustentaculum bore the whole weight of the leg transmitted through the astragalus, articulated distally by a concave facet with the cuboid. The cuboid supported mts. iv and v, the three sub-equal cuneiforms articulating respectively with mts. i, ii and iii. A very constant feature was the relative shortening of the mesocuneiform (*Phenacodus*), so that the proximal portion of the mt. ii was inserted between the endo- and ectocunei-forms. A similar facet may be present between mt. iii and the cuboid; these ectal facets being analogous to those upon mcs. ii and iii in the manus in not being of a supporting character; in other words, there was no true displacement between the podium and metapodium.

THE MANUS. There was in all probability a c e n t r a l e occupying the same posi-tion as in *Hyrax*, for this element has now been found both in the Hyracoidea and

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* Tertiary Vertebrata, p. 551.

† *Op. cit.*, p. 399: "This foramen is formed by the closing of the usual tendinous notch," etc.

‡ Dinocerata, p. 148.

§ Various papers upon the Cernaysien fauna.

‖ Baur, On the Morphology of the Tarsus in the Mammals, American Naturalist, Jan., 1885, p. 349. See also, Marsh, Dinocerata, p. 146.

Proboscidia.* The distal row of carpals was probably much broader than the proximal, and the metapodials, as in the pes, were without any lateral facets.

GENERAL MODIFICATION OF THE FEET.

The primitive structure, as Cope has shown, is approximately preserved in the plantigrade *Hyrax*, showing that all the secondary articulations in various ungulates were adaptations to digitigradism. There are four stages in the foot elevation: First, the p l a n t i g r a d e, already described; then the s e m i p l a n t i g r a d e, seen in the feet of the Proboscidia and Dinocerata, with short slanting metapodials well raised proximally. Rütimeyer has proposed "digitiplantigrade" for the reduced types with elongate vertical metapodials in which the phalanges rest fully upon the ground (*Camelus*). As this condition is practically analogous to that in one division of the Carnivora, it may be more simply described as d i g i t i g r a d e. There are of course many steps between this condition and the u n g u l i g r a d e foot, in which the terminal phalanges alone rest upon the ground (*Equus*).

The universal result of elevation of the wrist and ankle joints was d i s p l a c e - m e n t in some form, from the serial order, adapting the foot bones to the new inci- dence of impacts and strains. Then came reduction of one of the lower leg bones and of the lateral digits. With one exception, seen in the proboscidian manus, the departure from the serial type was upon a single principle: First,† the II and III m e t a c a r p a l s a n d m e t a t a r s a l s a c q u i r e d l a t e r a l s u p p o r t i n g f a c e t s u p o n t h e s e c o n d r o w o f p o d i a l e l e m e n t s, usually upon the outer side. Second, t h e b o n e s o f t h e u p p e r r o w o f c a r p a l s a n d t a r s a l s f o r m e d a r t i c u l a t i o n s w i t h t h e m o r e e c t a l e l e m e n t s o f t h e s e c o n d r o w.

In the general modifications of the MANUS it is important to note that mcs. II and III invariably acquired supporting facets upon the ectal side with the magnum and unciform respectively. Excepting in the semiplantigrade orders the reduction of the first digit was very rapid, it being already absent or functionless in the Eocene Diplarthra. The extension of the lunar was the next step in displacement; spreading upon the trapezoid in the Proboscidia, or upon the unciform, by its own growth or that of the unciform beneath it, in all other ungulates. This is incipient in *Phenacodus* and extensive in the Amblypoda. In other phyla the displacement of

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* Rütimeyer, Ueber einige Beziehungen zwischen den Säugethierstammen Alter und Neuer Welt, Zurich, 1888.

† See Marsh, Dinocerata, p. 183, § 2 : That the metapodial displacement was more primitive than the podial is shown both in *Phenacodus* and *Hyrax*, in which mcs. II and III abut laterally against the magnum and unciform, while the carpals are serial.

the scaphoid and lunar was probably concomitant.*   In the earliest known Diplar-
thra the scaphoid has a facet upon the magnum of the same width as that of the un-
ciform beneath the lunar—these facets increase, *pari passu,* until we reach the most
specialized forms.   In all the Perissodactyla the law of ectal displacement of the
metacarpals is maintained ; after mc. I disappears the trapezium persists ; as mc. II is
reduced it invariably retains its entire hold upon the trapezoid ; mc. III spreading
only to the ectal side (Kowalevsky).   In the adaptively reduced Artiodactyla, how-
ever, mc. III acquires a broad trapezoidal facet, forming an exception to the otherwise
universal rule.

The general modifications of the PES are still more interesting.   In the astragalus
the f l e x o r   f o r a m e n   disappeared, being for a long time represented by a groove ;
the primitive foot undoubtedly had a limited grasping power, the flexion being dis-
tributed between the metapodials and phalanges ; this was replaced by the greatly in-
creased play in the ankle joint and the development of the muscles inserted in the *tendo
achillis* as propellers.   The trochlear groove deepened, limiting the motion to the fore
and aft direction (Cope) ; the navicular facet became saddle-shaped and then flat, ex-
cepting in the artiodactyl phylum ; the sustentacular facet divided into two, which may
be called the "s u s t e n t a c u l a r" and "i n f e r i o r," producing three distinct cal-
caneal facets.†   The displacement of the astragalus and cuboid by reciprocal growth
was almost universal, having but two exceptions, in the Proboscidia, where the navic-
ular extended upon the cuboid, and in the lines of Perissodactyla, which tended to
monodactylism.   The calcaneum in several series acquired a fibular facet, the tuber
was elongated and the sustentaculum extended inwards.   While rarely in contact
with the navicular anteriorly (as in the primitive horses), the calcaneum in some

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* Upon this point hangs the question whether the diplarthrous foot ever passed through the amblypodous stage,
as held by Cope.   In the absence of any direct palæontological evidence, Schlosser (Beiträge z. Stammesgeschichte der
Hufthiere, p. 6) has strongly insisted upon the direct derivation from the Condylarthra upon the ground of the dis-
similarity both in foot and tooth structure.   His objections, though well taken, indicate a misunderstanding of Prof.
Cope's taxonomic principle of selecting genera at a certain stage of evolution in foot or tooth structure, to form a family
or order, irrespective of actual descent or relationship.   When, upon this system, the derivation in question is main-
tained, no genetic relationship of the Perissodactyla and known Amblypoda is thereby implied, but that at one stage
in the evolution of the diplarthrous foot the lunar rested widely upon the unciform, as in *Coryphodon,* the scaphoid
not reaching the magnum.   This proposition seems to us highly improbable, for we must suppose that the lunar first
extended upon the unciform while retaining its entire magnum facet, then it became reduced while the scaphoid ex-
tended upon the magnum—this hypothesis is rendered improbable by the fact that in all the early Diplarthra the
scapho-magnum and lunar-unciform facets are subequal.   The proboscidian manus is an exact counterpart to the
amblypod manus, and shows that the latter is to be considered not as in an intermediate but as in a final stage of de-
velopment.

† It is interesting to note the close parallelism to these adaptations to digitigradism in the Carnivora ; we observe
an entirely analogous division in these facets and evolution of the ankle joint.

series acquired a posterior navicular facet. The reduction of the entocuneiform followed that of mt. I. The fifth digit was much more rapidly reduced than in the manus. Independently of these reductions, mt. II and mt. III formed oblique supporting facets with the ectocuneiform and cuboid respectively analogous to the "alternating" metacarpal articulations, but the metatarsal articulations were much more variable than the metacarpal. As a general rule metatarsal displacement and growth was to the ectal side, the exception being in the Equidæ, where mt. III extended rapidly over the mesocuneiform.

The *metapodials*. In all the perissodactyls, primitive artiodactyls, and inadaptively reduced artiodactyls we find, as above stated, but one a l t e r n a t i n g type of metacarpo-carpal articulation; the adaptively reduced artiodactyls develop a second type of metacarpal articulation. In the *pes*, beginning with the "s e r i a l" type of *Phenacodus*, we find that genera tending to monodactylism develop what may be called the "p l a n e - s e r i a l" type, in which there is for a period no lateral spreading (*Hyracotherium*). The "r e v e r s e" type is exemplified in *Aphelops* and *T. indicus*, in which the second and fourth metatarsals both acquire ectocuneiform facets. The a l t e r n a t i n g type is developed in the *Titanotherium* tarsus and some other Diplarthra precisely as in the carpus. Each of these types has, of course, its functional significance.

We may now consider some of the special characteristics of the manus and pes in the five side lines. While observing many features which point back to the common taxeopod stem form, there are few or none which indicate any nearer mutual affinity than this.

II. THE HYRACOIDEA, AMBLYPODA, PROBOSCIDIA, Etc.

1. HYRACOIDEA.

An important fact is brought out by the comparison of the feet of *Hyrax* and *Dendrohyrax*. The manus and pes are absolutely plantigrade. In both, the carpals are arranged in strictly serial order, as described by Cuvier and Cope, although the metacarpals show decided lateral displacement. But in the tarsus of *Hyrax* the calcaneum rests exclusively upon the cuboid, and, as in *Phenacodus*, the calcaneo-cuboidal articulation is actually in some cases below the level of the astragalo-navicular.* In *Dendrohyrax* (*H. arboreus*, Princeton Museum), also from the Cape, t h e

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* These relations were found by removing the skin and fascia from the foot of a dried specimen in the Cope Collection. De Blainville's figures of *H. capensis* and *H. syriacus* show these facets on the same level.

a s t r a g a l u s h a s q u i t e a b r o a d c u b o i d a l f a c e t. The striking difference in the pes of these two genera bears directly upon the question of the taxonomic value to be attached to these articulations.

Other features of the feet are the interlocking tibio-astragalar joint, the probable presence of a *tibiale*, the *centrale* in the carpus, the reduction of mts. ɪ and ᴠ in the pes.

2. AMBLYPODA.

Cope has described the feet in this order as "plantigrade" ("Tertiary Vertebrata," p. 507). This term, which has also been generally applied to the proboscidian feet, should now be restricted to the types in which the entire foot rests on the ground. The Puerco *Pantolambda** was probably plantigrade. The position of the metapodials in the Pantodonta and Dinocerata as indicated in the figures of Marsh ("Dinocerata," p. 184) was analogous, the wrist and ankle joints in each being well raised from the ground. Our own study of the tarsals of *Coryphodon* has, however, convinced us that the p e s was almost plantigrade, while the manus was semi-plantigrade.

The metacarpals ɪɪ and ɪɪɪ are displaced, alternating upon the magnum and unciform. The intercarpal displacement is unique; the lunar has a broad foothold upon the unciform, while the scaphoid has either no magnum facet (*Coryphodon, fide* Cope) or rests by a considerable posterior facet upon the magnum† as in some species of *Uintatherium*. The cuneiform rests partly upon mc. ᴠ.

In the t a r s u s Baur called attention to the facet probably for the *tibiale* upon the astragalus of *Coryphodon* ‡ and *Uintatherium*. The displacement is extreme, the astragalus extending the entire breadth of the foot in front, covering both the navicular and three-fourths of the cuboid. The astragalar foramen is frequently present in *Coryphodon* (see Cope, *loc. cit.*) and in *Uintatherium* (see Marsh, "Dinocerata," p. 148). The calcaneum has the primitive ectal and sustentacular facets, and the fibula occasionally came in contact with it (*Uintatherium*, Marsh, *op. cit.*, p. 152). The metatarsal articulation is of the "reverse" type, mts. ɪɪ and ɪᴠ articulating laterally with the ectocuneiform. The Amblypoda with unreduced digits, very short spreading

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* Placed by Cope in the Amblypoda.

† In his definition of the Amblypoda, Prof. Cope says ("Tertiary Vertebrata," p. 378) : "Scaphoid supported by trapezoid and not by magnum, which with unciform supports the lunar." See also, Amer. Naturalist, Nov., 1884, p. 1110. While this definition may apply strictly to *Coryphodon*, it cannot to *Uintatherium*. Of three carpal series in the Princeton Museum, two show a broad scaphoid facet upon the posterior half of the magnum, the third has none In Marsh's "Dinocerata," the lithographic figure on Plate LIV is incorrect ; the wood-cut, Fig. 152, is approximately correct ; the scapho-magnum facet is not indicated in Fig. 113, but is well shown in Plate XXXIV, Fig. 5, see page 113.

‡ Cope, however, separates *Coryphodon* by the absence of a tibiale, from *Bathmodon*, in which it is present.

metapodials and peculiar carpal displacement, a foot type adapted to animals of heavy bulk, really present a striking analogy to the Proboscidia and an intermingling of primitive with acquired characters.
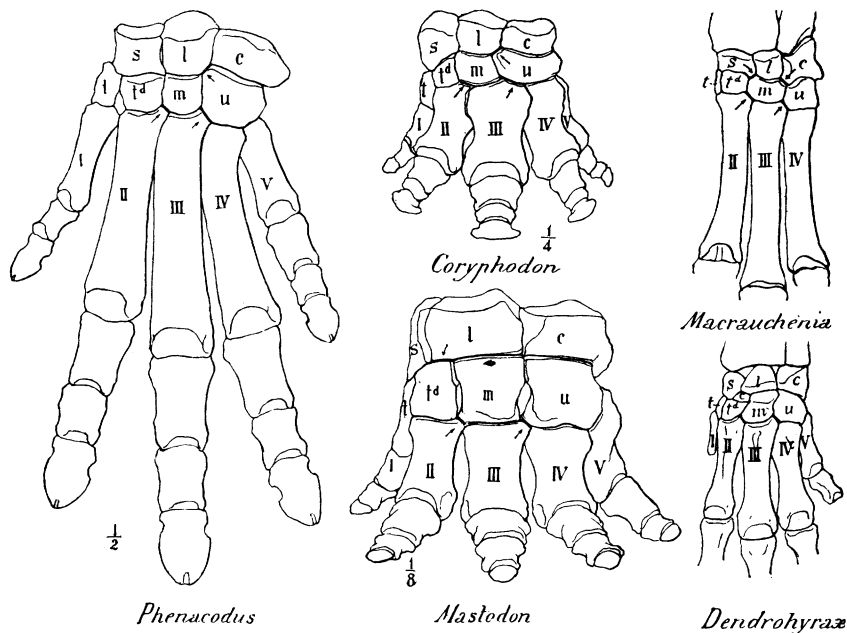
DIAG. 8.—The displacement of the bones of the manus in the Ungulata, I. *Phenacodus primævus,* from original in the Cope collection. *Coryphodon hamatus,* after Marsh. *Dendrohyrax arboreus,* from original in the Princeton collection. *Macrauchenia patachonica,* after Gervais. *Mastodon Americanus* from original in Princeton collection. The oblique arrows indicate the direction of displacement.

3. PROBOSCIDIA.

Weithofer* has recently directed attention to the unique departure from the tax- eopod condition of the carpus in this order—the lunar spreading upon the trapezoid, *i. e.,* to the ental side, instead of upon the magnum. In *Mastodon arvernensis, Ele- phas meridionalis* and *E. antiquus* from one-fourth to one-fifth of the inferior face of the lunar rests upon the trapezoid. We find the same condition in *Mastodon Americanus.*

This author attributes this to the enlargement of the ulna and its extension upon the lunar *vs.* the radial enlargement in all other ungulates. This displacement is variable, since it actually recedes and sometimes disappears (*op. cit.,* p. 515) in the adult recent forms (*E. Indicus, E. Africanus*). Burmeister moreover has figured† the carpus of a specimen of *M. Humboldtii,* in which the lunar spreads both upon the trapezoid and magnum. Another primitive feature of the carpus is the recently

* Einige Bemerkungen über den Carpus der Proboscidier. Morph. Jahrb., 1888, p. 507.
† Ann. del. Mus. Publ. d. Buen. Ayres, Plate XIV, p. 287.

discovered centrale.* The distinctive features of the tarsus have long been recognized, viz., the extension of the navicular with the astragalus above the cuboid, and the fibulo-calcaneal facet.

4. Toxodontia.

Prof. Cope† has found a striking resemblance to the proboscidian pes in *Toxodon*. The astragalar and fibular facets of the short c a l c a n e u m are subequal and face upwards, the cuboid facet is on the inferior face of the extremity of the calcaneum and faces downward. The a s t r a g a l u s has probably no cuboid facet; its navicular facet is plane and truncates the bone somewhat inferiorly as well as distally. The metapodial elements are robust and short, the distal metatarsal keels are posterior and rudimental; the proximal faces have lateral facets indicating a slight displacement. The number of digits is uncertain, the lateral ones are reduced in length, but robust. "The posterior feet were more truly plantigrade for the extremity of the calcaneum reached the ground." The instep was raised, forming an arched angulate type of foot. If this description is correct, this foot is more primitive than that of the Proboscidia.

5. Macrauchenia.

The feet of *Macrauchenia* have some striking peculiarities. The lateral displacement in the carpus and tarsus so characteristic of all the Perissodactyla is absolutely wanting in the tarsus and aberrant in the carpus. As Burmeister pointed out in his most recent paper‡ (p. 263) a gap exists in the usual point of junction of the calcaneum, cuboid, astragalus and navicular. The a s t r a g a l u s is entirely separated from the cuboid and even from the calcaneum, the navicular participating in this separation. His description and figures strikingly suggest the arrangement of the tarsals of the dog in this region. The c a l c a n e u m has but two astragalar facets, the sustentacular and inferior having coalesced, as in some species of *Palæotherium*, *Rhinoceros*, and the Hyracodontidæ; its distinctive feature is the extensive fibular trochlea, very similar to that in the Artiodactyla, and functionally unlike those observed in the primitive Equus and Titanotherium series. The c a r p u s is also

* Rütimeyer, *op. cit.*, page 11, foot-note.

† Note on the Structure of the Posterior Foot in *Toxodon*. Proc. Am. Philos. Soc., April, 1881, p. 402.

‡ Neue Beobachtungen an Macrauchenia Patachonica. Nova Acta der Ksl. Leop.-Carol. Deutschen Akademie der Naturforscher, Bd. XLVII, Nr. 5, pp. 239–267 (Nachträgliche Beschreibung der Fusswurzel von Macrauchenia). Also, Descripcion de la Macrauchenia Patachonica. Ann. del. Mus. Publ., Buenos Ayres, Tom. i, p. 32–66.

unique, in the fact that while the scaphoid has acquired an extensive magnum facet, the lunar is extremely small; the magnum is large and not only excludes the lunar from the unciform, but actually has a cuneiform facet. Burmeister describes facets for lateral digits upon the pes.* The metapodials are strongly keeled.

Schlosser† lays great stress upon the primitive character of this animal as shown in the serial disposition of the foot bones and the epicondylar foramen of the humerus. In his earlier paper (Zool. Anz., p. 683), he placed this genus with the Perissodactyla; later he separated it : "Fasst man alle diese Merkmale zusammen, so kann man kaum entschliessen *Macrauchenia* den Perissodactylen beizuzählen" (Morph. Jahrb., Bd. XII, 1886, p. 22). Upon this it may be observed that the arrangement of the carpals is not serial, as he intimates, but has a peculiar adaptive displacement. The fibulo-calcaneal facet may be considered a secondary character (see p. 533). We can in fact only conjecture the phylogenetic position of this genus, with its extraordinary mixture of characters. Upon the whole it is more nearly related to the perissodactyl than to any other phylum, and is possibly an offshoot of the primitive mesaxonic stem, separating from the main line at a period corresponding to the Wasatch.

III. THE PERISSODACTYLA.

When we examine the Diplarthra as a whole, after reviewing the unrelated and widely divergent groups which have already been considered, in which the displacement of the carpals and tarsals presents little or no analogy, we find in contrast a very striking uniformity in the displacement of the upper elements to the outer side, *i. e.*, in the carpus, the s c a p h o i d a r t i c u l a t e s w i t h t h e m a g n u m i n t h e s a m e d e g r e e t h a t t h e l u n a r a r t i c u l a t e s w i t h t h e u n c i f o r m; in the tarsus, the a s t r a g a l u s i n v a r i a b l y e x t e n d s u p o n t h e c u b o i d. This is the universal law of displacement which is subject to variation in degree only. It characterizes the stem forms of every family, and is secondarily modified by growth arising from special causes.

We may begin with a type in which the displacement is least extreme, and will here consider only the Perissodactyla.

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* *Op. cit.*, p. 265, "Obgleich *Macrauchenia* nur drei vollständige Zehen an jedem Fusse besitzt, so sind doch Resten von zwei anderen, wenigstens am Hinterfusse vorhanden gewesen, wie die Gelenk-facetten am Astragalus und Navicu-lare, gleich wie am Cuboideum beweisen."

† Zur Stammesgeschichte der Hufthiere. Zool. Anzeiger, No. 210, 1885, p. 683. Also, Beiträge zur Kenntnis der Stammesgeschichte der Hufthiere. Morph. Jahrb., Band XII.

1. THE TAPIR SERIES.

In *Isectolophus* (No. 10,401, Princ. Coll.), from the Uinta beds, we have a genus which is in or near the line of the true tapirs. It is represented by the almost complete carpus and a single element of the tarsus, the cuboid. (See full previous description, also Pl. X, Fig. 3.)

The *carpus*. The elements of the carpus are broad relatively to their height. The scaphoid has a horizontal trapezoid facet and slightly oblique magnum facet; thus its main weight is borne by the former bone. The lunar is large and has a slightly larger unciform than magnum contact, but it may be said to rest equally upon these bones. The cuneiform divides the upper surface of the unciform with the lunar. The magnum articulates with the scaphoid, lunar, trapezoid, unciform, and distally with the metacarpals II and III. The carpo-metacarpal articulation is of the usual alternating order. The unciform has inferior facets for metacarpals IV and V.

The *tarsus*. The cuboid is subquadrate in shape when viewed from in front and from above and proximally has a small astragalar facet.

No intermediate forms have been described. The manus and pes of the recent *Tapirus indicus* do not show a very wide divergence from the type above described. The scaphoid is enlarged posteriorly and besides its trapezium facet has subequal and horizontal trapezoid and magnum facets. The lunar has a relatively larger unciform facet, but still rests directly upon the magnum by a horizontal facet which is variable in width. The cuboid is subquadrate and partly supports the astragalus. The tarso-metatarsal articulation varies in different species. In *T. indicus* both mts. II and IV abut against the ectocuneiform.
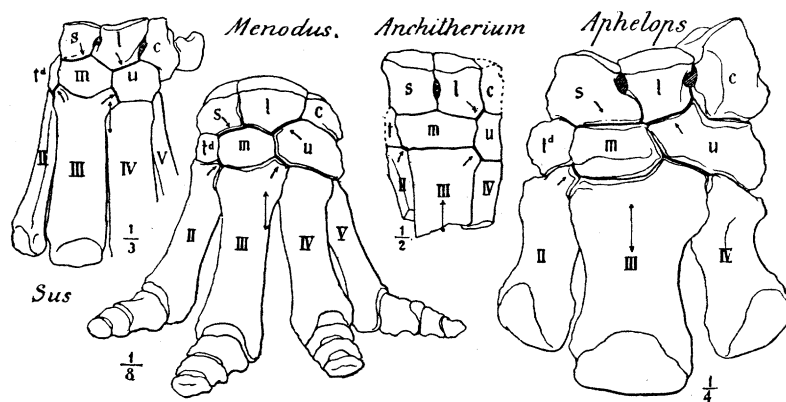
DIAG. 9.—The displacement of the bones of the manus in the Ungulata, II. *Sus scrofa*, illustrating the typical adaptive displacement in the Artiodactyla. *Titanotherium* (*Menodus*), from original in Harvard collection; *Anchitherium aurelianense*, after Kowalevsky; *Aphelops*, from original in Harvard collection. The oblique arrows indicate the direction of displacement; the double vertical arrows indicate the mesaxial line of the foot.

2. THE EQUUS SERIES.

The equine series is the most complete known, and is well distinguished from the others by the fact that the effects of lateral displacement in the carpus, which are well advanced in the Eocene members, although never extreme, are subsequently counterbalanced, and practically lost sight of, in the growth of the bones in the median line resulting from monodactylism. In the tarsus the displacement is very limited and is not similarly retrogressive. It is surprising to note the constancy in size and shape of the small astragalo-cuboid articulation from the Wasatch *Hyracotherium* to the recent horse; secondly, the early appearance of minor equine marks in the manus and pes. The displacement or diplarthrism is thus limited in both feet. The important secondary characteristic is the backward rotation of the lateral elements of the carpus, tarsus and metapodials.

CARPUS. The distinctive feature is the fact that the scaphoid early gains a somewhat broader foothold upon the magnum than the lunar has upon the unciform. This may be attributed to the early enlargement of mc. III, and ectal growth of the magnum. The lunar in the Eocene members retains subequal magnum and unciform facets (as in *Isectolophus*), but the carpus is laterally compressed. In the more recent forms the magnum, by its rapid growth, extends beneath the lunar, and the latter bone is thus brought back to its primitive position and rests in some species exclusively upon the magnum.

Hyracotherium and *Epihippus*. There is no marked difference between the carpus of *H. venticolum* and of *Epihippus*, excepting the advanced reduction of mc. v. In *Epihippus* (No. 10,405, Pl. XI, Fig. 4), the bones of the upper row are elongate. The s c a p h o i d is directed backwards and rests distally upon the trapezoid and magnum, by subequal horizontal facets. The trapezium contact is very small. The l u n a r has the high and slender proportions seen in *Triplopus*, but the distal facets for the magnum and cuneiform are subequal and incline obliquely towards each other. The cuneiform is narrow and slender. The trapezium was evidently small, articulating with the scaphoid, trapezoid and mc. II. The trapezoid is much flattened. The m a g n u m supports the lunar anteriorly and posteriorly. The u n c i f o r m has an infero-lateral facet for the fifth metacarpal. The foot is practically tridactyl, mc. v being well retracted. The metacarpal articulation is of the a l t e r n a t i n g type.

The carpus of *Mesohippus* has never been described, nor that of any American species of *Anchitherium*. Referring to Kowalevsky's Memoir (Pl. II, Fig. 1a), we observe that the m a g n u m extends beneath three-fourths of the lunar and the same proportion of the scaphoid, yet the metacarpal articulation is unaltered, mcs. II and

III forming "alternating" lateral contact with the magnum and unciform respectively. Kowalevsky, however, describes mc. III as spreading posteriorly beneath both the trapezoid and unciform. Thus the spreading of the magnum has already offset the progress of the more primitive displacement. A further step is seen in *Hipparion*.

If De Blainville's figures are correct (*G. equus*) the recent species, *E. caballus*, *E. Burchellii* and *E. asinus*, present three stages in the growth of the magnum beneath the lunar. In the former there is a broad contact between the lunar and unciform, much as in *Hipparion;* in the latter there is none at all, the lunar resting wholly upon the magnum, as in the primitive serial type.
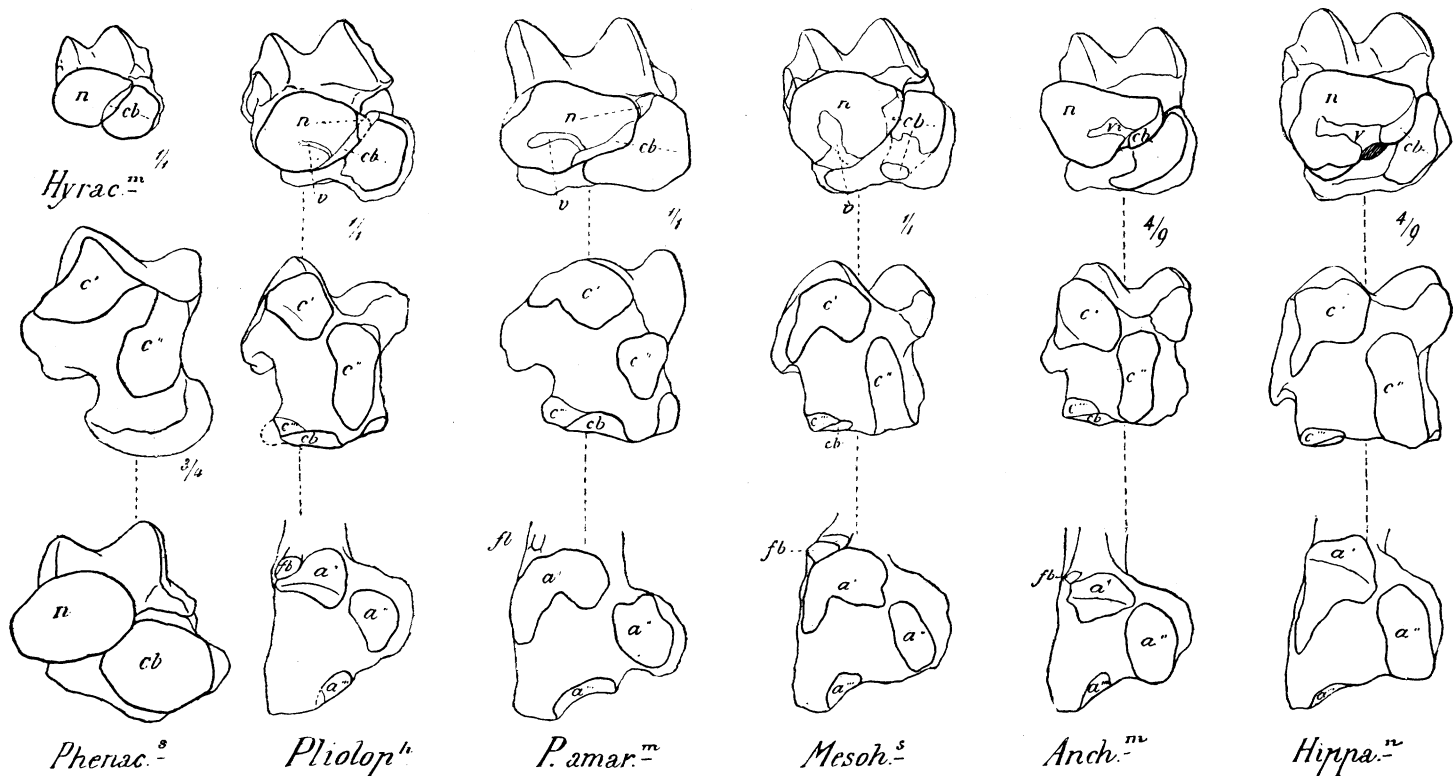
DIAG. 10.—The evolution of the astragalar and calcaneal facets in the Hyracotherium-Hipparion series. *Phenacodus primævus*, Cope collection ; *Hyracotherium venticolum*, Cope collection ; *Pliolophus* (Orohippus) *major*, Princeton collection ; *P.* (Triplopus) *amarorum*, Cope collection ; *Mesohippus*, Princeton collection ; *Anchitherium aurelianense*, Princeton collection ; *Hipparion mediterraneum*, Princeton collection. The upper row represents the distal view of the astragalus and calcaneum ; the middle row the posterior view of the astragalus ; the lower row the anterior view of the calcaneum. *a', a'', a'''*, ectal, sustentacular and inferior astragalo-calcaneal facets. *c', c'', c'''*, ditto calcaneoastragalar facets. *cb, fb, n*, cuboidal, fibular and navicular facets upon astragalus and calcaneum. *v*, fossa in the astragalo-navicular facet.

The reduction of the metacarpals is too familiar ground to require description here.

TARSUS. In the tarsus we fortunately have a complete series from *Hyracotherium* upwards. We begin with a tridactyl pes, although in the Wasatch species *H.*

validus (Marsh), there is a remnant of mt. I.* In the Eocene genera the separate elements are very narrow and vertically elongate; later the elements become broad and spreading. A primitive and persistent feature is the triangular cuboidal facet upon the astragalus (see Diag. 10). Another marked characteristic, early developed, is the reduction in size of the "inferior" astragalo-calcaneal facet and its wide separation from the "sustentacular." An important equine mark is the depression or fossa in the astragalo-navicular facets; this is a slight valley (*v*) in the Bridger species of Hyracotherium, which is variable in size but constantly increasing in the ascending series, terminating in an extensive fossa, in *Equus*.

There are, moreover, a number of minor tarsal features not always persistent but of great value in diagnosis; the three astragalo-calcaneal facets (*c'*, *c''*, *c'''*) are always separate, the trochlear groove is deep and sharp. In many Eocene species the navicular is inserted anteriorly between the cuboid and astragalus and thus develops a distinct calcaneal facet; this feature does not persist. In all Eocene specimens the calcaneum has a distinct pit for the fibula, in extreme flexion; this is usually facetted; it reappears in *Mesohippus* and sometimes persists in *Anchitherium*.†

The metatarsal articulations pass through three distinct types. In the Eocene genera we find the "alternating" type, in the Miocene the "plane serial," replaced later by the equine type.

Hyracotherium venticolum, Pliolophus and *Epihippus*, the Eocene genera, may be considered together. The first species from the Wind River is distinguished by the absence of the fossa in the astragalo-navicular facet (Cope, "Tert. Vert.," p. 645); this fossa is more or less distinct in five small and two large astragali (*P. pumilus* and *P. major*), in the Princeton collection, from the overlying Bridger, and very distinct in the *P.* (*Triplopus*) *amarorum* of the still more recent Washakie (Cope Coll.). The fibulo-calcaneal pit is present throughout, but is not invariably facetted. The naviculo-calcaneal facet is not present in *H. venticolum;* it appears in *P. major* and *P. amarorum*, but not apparently in *P. pumilus*. The highly compressed tridactyl character of the foot is retained throughout. The mts. III and IV articulate exclusively with the ectocuneiform and cuboid respectively. Mt. II articulates proximally with the mesocuneiform, also laterally with the ento- and ectocuneiforms. These relations are seen in *H. venticolum* and in *P. major*. In *P. amarorum*, mt. IV articulates laterally with the ectocuneiform. This species is also distinguished by the flattening of the navicular and cuneiforms and relative shortening of the cuboid.

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* Marsh, Am. Jour. Sc. and Arts, Nov., 1876, p. 401.

† This facet is well marked in a calcaneum lately received in exchange from the Paris Museum, marked *A. aurelianense*, from Sansan. See Diag. 10.

Through the Eocene series, the lateral toes are not more rolled backwards than in *H. venticolum.*

In *Mesohippus,* the most marked development is seen: first, in the flattening of the cuneiforms; the entocuneiform is united with the mesocuneiform, but does not support mt. ii; second, the tarso-metatarsal articulation is absolutely of the plane serial type; third, the lateral digits and corresponding tarsal elements are rolled backwards so that the outer elements are almost or quite in contact posteriorly, the cuboid touching the entocuneiform. The fibulo-calcaneal facet is always distinct. In the a s t r a g a l u s the ectal and sustentacular facets become nearly confluent; the astragalo-cuboidal facet is reduced to a small narrow triangle placed in front. The seven astragali examined (Princeton Coll., No. 10,255), apparently represent two species, in one of which, the smaller, the fossa upon the astragalo-navicular is faint; the larger species shows this fossa very distinctly (Prince. Coll., No. 10,256). This may, however, be not a specific but an age character.

The serial metatarsal articulation is an extremely interesting feature, when we compare this tarsus with that of *Hyracotherium* and *Pliolophus;* it precedes the growth of mt. iii upon the cuboid in *Anchitherium,* an altogether different process from the lateral displacement seen in the above Eocene forms.

It is not necessary here to go over in detail the ground made familiar by the memoirs of Kowalevsky and Forsyth Major,* of the subsequent evolution of the pes; in fact, the material from American strata for such a purpose is not at present accessible.

3. The Hyrachyus, Triplopus, Hyracodon Series.

There is an intermingling of rhinocerotic and equine characteristics in the teeth and feet respectively of this series, which give it an especial interest and separate it widely from both the above stocks. It has nothing in common with the tapir series either in the structure of the teeth or feet, and unlike both the tapirine and equine lines, little is known of the sub-Bridger forms, and there is no parallel European phylum.

The general characteristics of the carpus and tarsus are the vertical elongation and lateral compression of the elements of each and the close union of the metapodials in some of the later forms, which, while tridactyl, renders the foot in some forms functionally monodactyl.

* According to Kowalevsky (Anchith., Pl. II, Fig. 20A . .), the ecto- and mesocuneiforms unite in *Anchitherium,* but are distinct in *Hipparion* (Anthracother., p. 164). According to Forsyth Major (Beit. z. Gesch. d. foss. Pferde. II Th., p. 62), the union of cu. 1 and 2 is the rule and of cu. 2 and 3 the rare exception.

CARPUS. In the tetradactyl *Hyrachyus* we find all the distinctive features of the carpus in this series are practically attained, these resulting from the great lateral displacement. The s c a p h o i d has a very narrow trapezium facet and broad and decidedly oblique trapezoid facet; it rests broadly upon the magnum. In the l u n a r the radial facet is shallow; it is compressed below, with a narrow oblique anterior facet upon the magnum and broad subhorizontal unciform facet. The scaphoid and lunar thus rest principally upon the magnum and unciform. The cuneiform presents a small ulnar facet, this bone being rather slender. The trapezoid has a broad trapezium facet. The magnum has a narrow and oblique lunar facet. The unciform is a very characteristic bone since its vertical is greater than its transverse diameter. It nevertheless has a narrow facet for mc. v, which, according to Cope, is considerably the most slender.

Taken altogether the vertical and transverse diameter of the carpus is about the same.

In *Triplopus* the vertical diameter of the carpus is slightly greater than the transverse, the metapodials and carpals are somewhat rolled backwards so that the anterior face of the manus is strongly convex. Every feature in which the manus departs from that of *Hyrachyus* is in the direction of greater elongation and lateral displacement. The s c a p h o i d is narrow and has a very oblique trapezoid facet; its main weight descends upon the magnum. (The small trapezium and the trapezoid are missing in the Princeton collection.) The l u n a r rests entirely upon the unciform, its contact with the magnum anteriorly is by a vertical facet, variable, never in the nature of support, sometimes entirely wanting. The c u n e i f o r m, like the scaphoid, is rotated backwards. Judging by the facets upon the mc. II and the scaphoid, the trapezoid was laterally compressed. The vertical diameter of the unciform exceeds the transverse; it still bears a considerable mc. v facet.

In *Hyracodon*, the carpus repeats the structure of *Triplopus* upon a larger scale. The proportions of the metapodials are approximately the same; the proximal portion of mc. v persists but is very much reduced in size. The m a g n u m has relatively increased in size, but still has a very limited contact with the lunar anteriorly. The trapezium is small and has no contact with mc. II. The vertical diameter of the unciform much exceeds the transverse; the cuneiform is also high and very narrow. The degree of backward rotation of the lateral elements evidently varies in the different species.

TARSUS. In the astragalo-cuboidal articulation, in the number and disposition of the digits and in the shape of the terminal phalanges, this series closely approaches the equine series, and, in some cases, can be distinguished only by very careful

examination.* The diagnostic features of the members of the *Hyrachyus* series are the relatively flat or obtuse keels of the trochlea and the frequent confluence of the sustentacular and inferior calcaneal facets of the astragalus. The same facets are invariably separate in the equine series, beginning with *Hyracotherium*. The *Hyra-chyus* calcaneum occasionally shows a pit for the fibula, but this does not bear a facet as in nearly all the equine series.
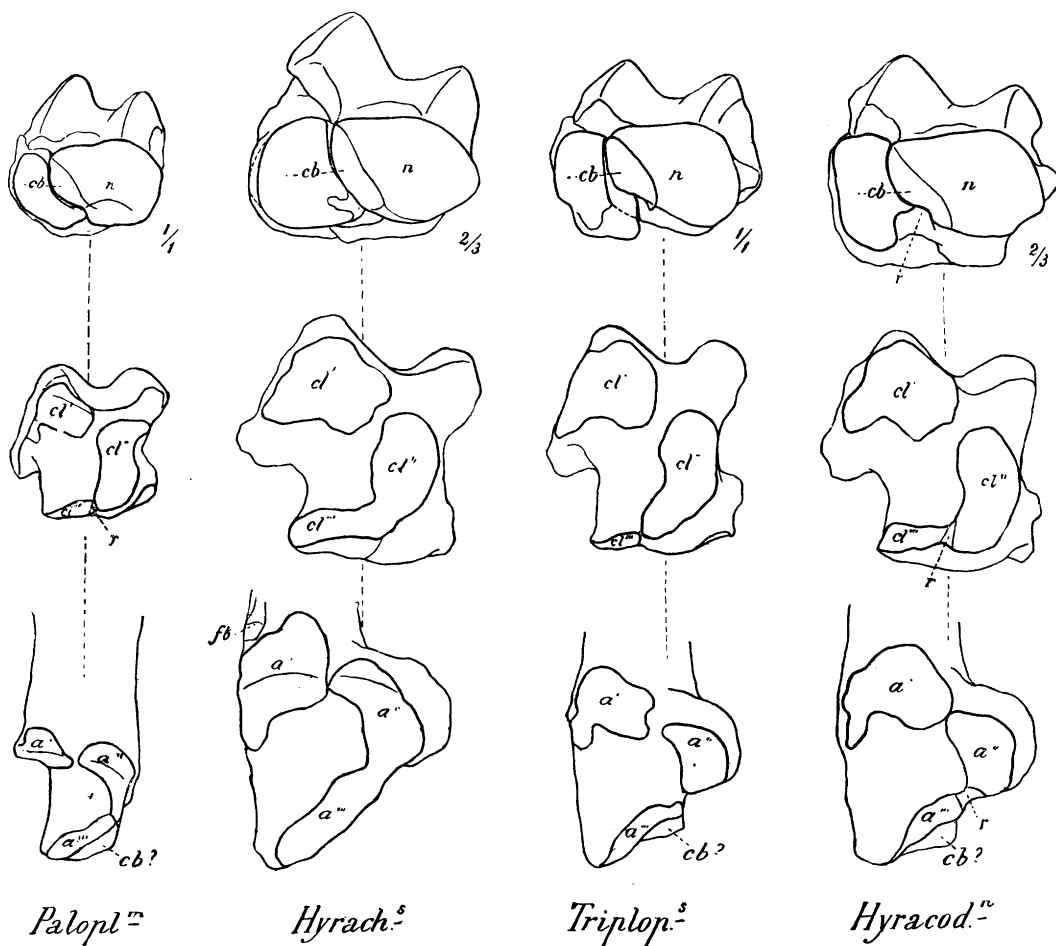
Diag. 11.—The astragalar and calcaneal facets in the Hyrachyus-Hyracodon series. *Paloplotherium minus*, Princeton collection. *Hyrachyus* (sp. indet.), Princeton collection. *Triplopus obliquidens*, Princeton collection. *Hyracodon major*, Princeton collection.

Hyrachyus (No. 10,199, Princeton Coll.). The cuboidal contact with the astragalus expands posteriorly, but is very narrow anteriorly in some species (*H. princeps*), bringing the navicular into contact with the calcaneum precisely as in some species of *Hyracotherium* (*Triplopus amarorum*) ; as above stated there are

* I have referred the *Triplopus amarorum* of Cope, from the Washakie beds (uppermost Bridger), to the equine series.

but two calcaneal facets, the inferior and sustentacular being confluent; the variants in these facets, seen by comparing a large number of astragali, are found to be: (1) The greater or less union of these facets, looking towards a more primitive form in which they were probably separate; (2) the presence of a small ridge, *r*, at the point of junction, looking towards the well-developed ridge in the later forms (*Hyracodon*). The c a l c a n e u m presents a very long slender tuber, three astragalar facets and an extremely narrow and deep distal cuboidal facet. The c u b o i d is correspondingly narrow and elongate, in the small species compressed in the middle, and with no trace of a facet for mt. v and little or no contact inferiorly with mt. iii. The e c t o c u-n e i f o r m is elevated and has a lateral facet for mt. ii. The m e s o c u n e i f o r m is small; according to Cope, "the e n t o c u n e i f o r m is large, flat and posterior in position." *

Triplopus (No. 10,397, Prince. Coll.). Although the pes as a whole is very narrow and slender, the trochlea is much shallower than in the equine series (Diag. 11, Plate XI, Fig. 9); the cuboidal contact narrows anteriorly to a point, but the navicular is excluded from contact with the calcaneum; the inferior and sustentacular facets are either confluent or closely approximated and vary in the development of the ridge (*r*). The c a l c a n e u m has a narrow and oblique cuboidal facet, a long laterally compressed tuber and narrow sustentaculum; there is no trace of a fibular facet. The c u b o i d is compressed in the middle as in *Hyrachyus*, elongate and with a relatively small distal facet for mt. iv, indicating that this digit was much reduced. The navicular is very deep and laterally compressed. The meso-cuneiform and entocuneiform are wanting in the Princeton collection. The ecto-cuneiform articulates with mt. iii only, indicating that the metapodial articulation was absolutely plane; the lateral toes were rotated backwards precisely as in *Anchitherium*.

Hyracodon † (No. 10,397, Princeton Coll.). In this genus we find an exact repetition of the tarsus of *Hyrachyus* in considerably heavier form than in *Triplopus*, and with few modifications. The a s t r a g a l u s has the same limited cuboidal contact; the three calcaneal facets are nearly confluent, the "sustentacular" and "inferior" are fully so and a sharp ridge at their point of junction interlocks with a correspond-

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* Tertiary Vertebrata, p. 659; *H. eximius.*

† On the Skull o the Eocene Rhinoceros, Orthocynodon, and the Relation of this Genus to other Members of the Group. E. M. Museum Bull. No. 3, 1883, p. 17, "Hyracodon was a slender, long-limbed and slightly built animal with a long neck and delicate head. Its proportions were those of a Horse rather than of a Rhinoceros." p. 20, "In short, it was a cursorial Rhinoceros, and all its modifications went towards adapting it to swift locomotion * * * One can hardly help believing that had this line persisted, it would have resulted in a unidigital type, just as the tridac-tyl *Anchitherium* of the Miocene has terminated in the Horse."—W. B. SCOTT.

ing depression in the calcaneum. The navicular is shallower than in *Triplopus*, resembling closely that of *Hyrachyus*, and showing facets for three cuneiforms. The c u b o i d is elongate and compressed in the centre as in the above forms, and articulates distally with mt. IV only. The e c t o c u n e i f o r m has a lateral facet inferiorly for mt. II (unlike *Triplopus*), thus reverting to *Hyrachyus*. The m e s o-c u n e i f o r m is correspondingly shortened, while the e n t o c u n e i f o r m is flattened and rotated backwards as in *Hyrachyus* (No. 10,005, Princeton Coll.).

In the pes of *Paloplotherium* we have a striking resemblance to that of *Triplo-pus*, and of the Eocene horses except for the greater reduction of the lateral toes. This is simply an example of parallelism, for the teeth* show no affinity to either of these lines. The lateral digits are as far reduced as those of *Hipparion*.†

4. THE RHINOCEROS SERIES.

A.—Aceratherium.   B.—Aphelops.

The comparison of the carpus and tarsus in the hornless rhinoceroses of the American Miocene shows a wide divergence between the *Aceratherium* (lowermost Miocene) and *Aphelops* (uppermost Miocene) series. The *Aceratherium* feet are extremely elongate, with the toes closely compressed, reminding one strongly of the feet of the pseudo-rhinoceros, *Hyracodon*, from the same beds. The more recent *Aphelops* is generally considered a successor, but shows a widely different type of

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* Schlosser (Beiträge z. Stammesg. d. Huft.) points out the anomalous mixture of primitive and secondary characters in this genus. The premolars are reduced in number, ¾, but simpler than the molars, while the molar crowns are more advanced than those of *Palæotherium*, showing cement.

† Lydekker (Cat. Foss. Mamm., Part IV, p. 16) follows Flower in uniting *Paloplotherium minus* and *Palæotherium* (see Cat. Roy. Coll. Surg., Part II, Mammalia, p. 390). The ground assigned is the presence of a "complete transition between the two types." On precisely similar principles we should unite *Hyracotherium venticolum* with *Mesohippus*; nay more, because the American genera undoubtedly belong to one line of descent, whereas the two French genera, judging by the extremities and teeth, belong to different lines. Further, is nomenclature actually simplified when a genus is made so comprehensive as to extend over long geological and wide geographical areas, embracing such a variety of forms that it becomes necessary (*vide Rhinoceros* and *Palæotherium, opera citata*) to arrange the species into groups? We think not. Genera can no longer be defined in the Linnæan sense. Lamarck, a century ago, anticipated the difficulties which would arise when the gaps between Cuvier's and Buffon's genera were filled up. The range of variation which should be included in a single genus is largely a matter of arbitrary judgment. Never has the problem been more perplexing than among the unbroken series found in the western Tertiaries. The writers, for the present, have adopted the rule long since employed by Marsh and Cope, viz , differences of degree, size, proportion, may be taken as specific; differences of kind (in the number of teeth or digits) or of actual form (*e. g.*, the assumption of the molar pattern by the premolars), may be taken as generic. This rule, when applied, for example, to the horse series, is found to work admirably—each of the subdivisions of the Eocene is characterized by a genus—and by a number of species varying in the direction of the lower and higher forms. Judging by the thickness of the strata, these subdivisions represent long periods of time.

foot, which is highly "modernized." The relations of these genera to the European forms is somewhat uncertain, so that the following observations apply especially to the above American genera.

Amynod[n]   *Acerath*[m]   *Aphel*[s]
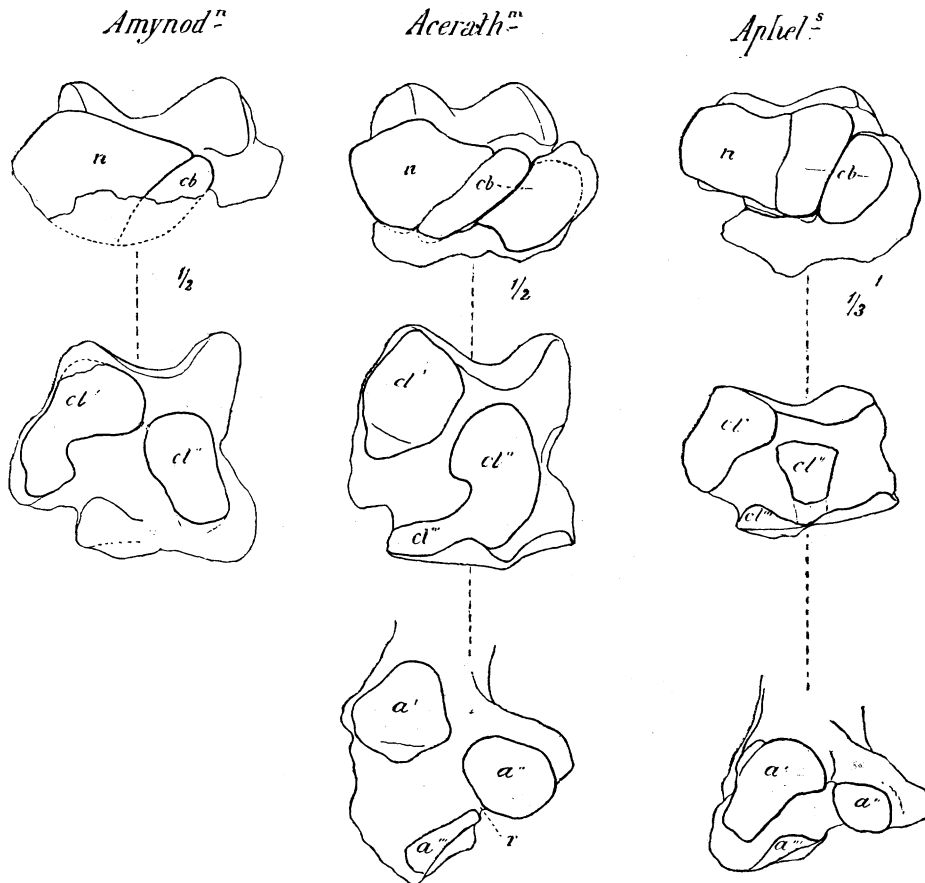
DIAG. 12.—The astragalar and calcaneal facets in *Amynodon*, *Aceratherium* and *Aphelops*. All species indeterminate.

A.—ACERATHERIUM (Coll. Mus. Comp. Zoöl.). The general characteristics of the feet are lateral compression and vertical elongation of the carpal and tarsal elements and the elongate character of the metapodials. The *carpus* shows the same degree of lateral displacement seen in the tapir. The scaphoid is subquadrate, resting by a broad and slightly oblique facet upon the trapezoid. The lunar has a broad unciform facet, but retains a small horizontal facet upon the unciform. The cuneiform extends widely backwards. In the second row, the trapezoid supports mc. II; the magnum is a stout bone, subquadrate anteriorly, projecting beneath the lunar posteriorly with the incipient stout pivotal peg, which is so largely developed in *Aphelops*. The third metacarpal is less enlarged than in *Aphelops*; the second and

fourth are slightly smaller; the unciform facet indicates that mc. v (missing in this collection) had about the same relative size as in the tapir.

The *tarsus*. The astragalus rests by a rather narrow facet upon the cuboid; this facet is equally broad posteriorly and anteriorly, as contrasted with the *Hyracodon* and equine series on the one hand and the *Palæosyops* series on the other. The arrangement of the calcaneal facets is shown in Diag. 12. The calcaneum has a long slender tuber expanding into a knob. The cuboid has its vertical diameter exceeding the transverse, unlike all the more recent rhinoceroses. The articulation of the third and fourth metatarsals with the ectocuneiform and cuboid is of the "plane serial" type, but mt. II abuts against the ectocuneiform.

B.—In *Aphelops* the carpus and tarsus are very broad and spreading and show the extreme of diplarthrism. In both, the metapodial articulation is of the primitive "alternating" type. The toes spread widely, being reduced to three in each foot.

CARPUS (see Diagram 8). The scaphoid is very broad, covering the whole anterior surface of the magnum, while the lunar rests anteriorly upon the unciform alone, posteriorly upon the pivotal process of the magnum. A remarkable feature of this bone is its unique articulation with the magnum hook posteriorly. The great development of the middle toe and relatively increased size of the magnum, renders the scapho-magnum surface broader than the lunar-unciform. Facets for the trapezium are seen upon mc. II and the trapezoid. The trapezoid and magnum facets of the scaphoid are subequal and horizontal, directly transmitting the weight. Mc. II abuts proximally against the magnum; mc. III is much larger than the lateral metacarpals and has a very broad unciform facet. There is no trace of a facet for mc. v.

This type of carpus is precisely similar to that of *R. unicornis* and *R. bicornis*, as figured by De Blainville.

TARSUS. The astragalus is broad and low with a shallow trochlea, and broad cuboidal facet, which is as large as that upon the calcaneum; a characteristic feature is the ental extension beyond the three distinct calcaneal facets. The calcaneum is characterized by a short tuber calcis and very slender sustentaculum; the three astragalar facets are separate and rather small. The transverse diameter of the cuboid is greater than the vertical. The mesocuneiform is much reduced. The mts. II and IV have lateral facets upon the ectocuneiform and cuboid respectively of the "alternating" type.

This type of tarsus is found in *R. unicornis* and *R. bicornis*, which are, however, less broad and spreading. These recent genera differ from *Aphelops* and resemble *Aceratherium* in the mode of metapodial articulation, the mt. III not possessing a cuboidal facet. In fact the cuboidal facet upon mt. III in *Aphelops* is apparently unique.

5. The Palæosyops, Diplacodon, Titanotherium Series.

The general characteristics of the feet in this series are the following: The carpus is broad and flat, and the lateral displacement is limited; there are four spreading and fully functional toes. In the pes on the other hand the cuboid extends rapidly beneath the astragalus, the lateral displacement being very rapid. The calcaneum has a fibular facet. The terminal phalanges are flat and spreading distally.

CARPUS. In each of the carpal elements in the genera of this series we invariably find (excepting in the lunar of some of the Bridger species) that the transverse diameter exceeds the vertical, in a ratio increasing as we ascend. The lunar can always be recognized by its nearly subequal magnum and unciform facets, and the unciform by its broad facet for mc. v.

Palæosyops (No. 10,013, Princeton Coll.). There are two distinct types of feet which may be here referred to *Palæosyops*, but cannot with certainty be determined specifically. One belongs to a large and heavy form with short, stout digits (possibly *P. major* Leidy, or *P. validens* Cope), the other to a lighter, more graceful animal with long, rather slender digits (possibly *P. paludosus* Leidy). There is a third type, intermediate in size, between the above, but showing the heavy proportions of the large type. The s c a p h o i d has subequal magnum and trapezoid facets, and, in its somewhat oblique position, transmits its weight equally to both elements. The l u n a r has a deep radial facet; it is wedge-shaped inferiorly; the direction of its magnum and unciform facet varies in the two types from a sharper to a more obtuse angle; thus, in the lighter forms the magnum facet is small and strongly inclined, while in the heavy forms the same facet is larger and more horizontal; corresponding variations are found in the superior facets of the m a g n u m; taken together they determine the degree of transmission of the weight through the magnum and unciform respectively. The t r a p e z i u m sustains no direct pressure, but articulates with the scaphoid, trapezoid and mc. II. The t r a p e z o i d receives half the weight of the scaphoid. The u n c i f o r m is very broad, resting inferiorly upon the mc. III-V. The variations in the metapodials between the heavy and slender types are strongly marked.

Diplacodon. The scaphoid, lunar and cuneiform of a carpus have been collected from the Uinta which agree so closely with the corresponding elements in the slender type of *Palæosyops* above described, that they require no further description. They belong either to a small species of *Diplacodon*, much smaller than the *D. elatus* of Marsh, or to a persistent species of *Palæosyops*. The only departure from the above

type is in the slightly increased massiveness, which might well represent individual variation.

The metapodials of a right manus of *Diplacodon* are well preserved; they are long, relatively slender, and spreading, interlocking closely proximally and keeled upon the posterior distal faces.

Titanotherium (Coll. Mus. Comp. Zoöl. of Cambridge). The growth of the lunar and magnum are the distinctive features of this carpus. The l u n a r presents two distal subequal facets for the magnum and unciform respectively. The c u n e i f o r m is relatively somewhat reduced, while the scaphoid is enlarged and rests by two nearly horizontal facets upon the trapezoid and magnum.
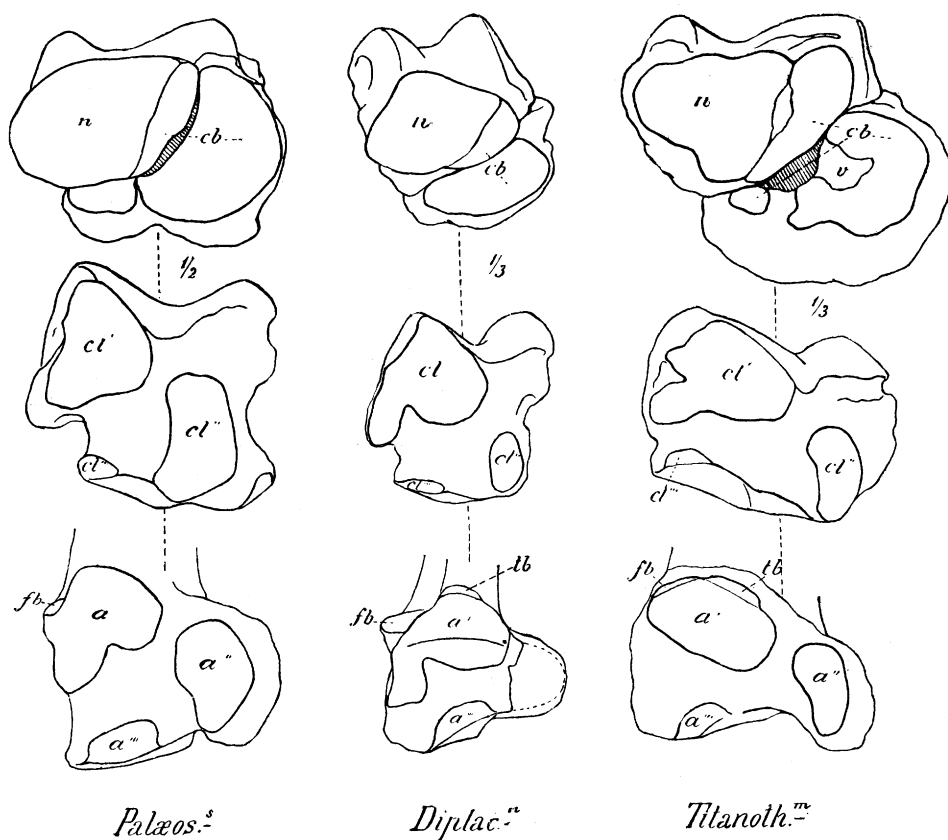
DIAG. 13.—The astragalar and calcaneal facets in the Palæosyops-Titanotherium series. *Palæosyops major*, Princeton collection; *Diplacodon ? elatus*, Princeton collection; *Titanotherium* (sp. indet.), Princeton collection.

Tarsus. The special characteristics of the tarsus, in addition to those above mentioned, are the wider separation of the three astragalo-calcaneal facets and reduction of the inferior facet; the astragalo-cuboid facet is an elongated triangle, broad in front, narrowing posteriorly; the astragalar trochlea extends backwards upon the

calcaneum so that the tibia articulates with the latter in *Diplacodon* and *Titanotherium*. The fibulo-calcaneal facet in *Palæosyops* increases to a considerable size in *Titanotherium*. The cuboid and other elements of the second row of tarsals are rather broad. The metatarsal articulation is secondarily of the alternating type.

Palæosyops. The astragalo-calcaneal facets together present a broad surface for the cuboid and navicular, between the bones is a gap which is bridged by the cuboid. The astragalo-cuboid facet is slightly narrower behind than in front. The c a l c a - n e u m has a small fibular facet, and distally presents a broad oval face for the cuboid. The cuboid is subquadrate in proportion, much as in the tapir series, and presents a sharply defined astragalar facet; distally it rests upon mt. iv, and presents a variable facet anteriorly for mt. iii. The ectocuneiform is also subquadrate anteriorly and not only supports mt. iii, but has a broad facet laterally for mt. ii. The mesocuneiform is thus somewhat flattened. The entocuneiform is not preserved in the Princeton collection.

Diplacodon. The tarsus (Plate VIII) is represented merely by an astragalus and calcaneum which are somewhat crushed, but nevertheless present important transition characters. Thus the fibulo-calcaneal facet is much larger; the tibia extends from the astragalar trochlea upon the calcaneum; the tuber calcis is very long and laterally compressed. In the a s t r a g a l u s the trochlea is deep; the three calcaneum facets are much reduced; the cuboidal facet is broader anteriorly and narrower posteriorly. There is thus an intermingling of *Palæosyops* and *Titanotherium* characteristics. Viewed together, however, these bones are elevated and laterally compressed, indicating a high and rather narrow pes. With the metacarpals above described, we may infer that *Diplacodon* had gained greatly in height upon *Palæosyops* without having acquired any of the massive proportions of *Titanotherium*.

Titanotherium. The tarsus is very broad and flat, the metapodials spreading widely. In the a s t r a g a l u s the trochlea is shallow, the inferior calcaneal facet is greatly reduced and is confluent with the cuboidal facet; the latter is broad in front and tapers to a point posteriorly. The gap between the astragalus and calcaneum, observed in *Palæosyops*, is here greatly enlarged, the cuboidal contact with both astragalus and calcaneum is interrupted by slight surface depressions, analogous to the "navicular fossa" in the horse. The tibia and fibula both have calcaneal facets. By the broadening of the cuboid the navicular is greatly reduced. The cuneiforms are flattened. Mt. iii has a broad contact with the cuboid, and mt. ii with the ectocuneiform.

In a general review of the above series, we observe practically the same type of intercarpal articulations in all tetradactyl and tridactyl forms irrespective of the geological period to which they belong. Thus the tapir manus is a persistent example of a type developed independently, at different periods, in *Hyracotherium*, *Hyrachyus*, *Aceratherium* and *Palæosyops*. The tridactyl rhinoceros, with *Triplopus*, *Hyracodon* and *Palæotherium* present another type. The significance of this parallelism is discussed in another section.

In the tarsus we find a striking analogy between the equine and Hyracodon series. In another series may be grouped all the remaining Perissodactyla.

There is actual disproof of Kowalevsky's generalization as to the bearing of the spreading of the metapodials upon the survival of the fittest, in the non-spreading of the metapodials at an important stage in the development of the horse series (see p. 546). In fact we can trace no connection between certain foot structures and survival in perissodactyl phyla. We must either with Schlosser (*op. cit.*, p. 121) regard the inadaptation of the teeth to the changes in the character of the food as the cause of extinction, or rather look at the organization as a whole in its relations to the changes both in food and to the rapid increase of Carnivora and competing Herbivora.

IV. THE CLASSIFICATION OF THE UNGULATES.

This detailed comparison certainly supports in a measure Rütimeyer's[*] designation of the foot bones as a " verschiebare mosaik," and raises the question as to how far these articulations can be employed in classification. With all the direct contradictions in Cope's system urged by Rütimeyer and others, which are here pointed out, there still remains the universal principle that in every step of transition from the primitive plantigrade foot towards digitigradism, some form of displacement from the serial order, or interlocking of parts, took place. This proceeded not at random, but along certain definite lines, conforming in general to the succession in geological time and large existing subdivisions of the Ungulata, and of great value as expressing their relations to each other and to the primitive stock. We cannot, therefore, as the distinguished Swiss palæontologist advises us (p. 18), rest content with the lines drawn by Cuvier and Owen, because the derivation from the plantigrade taxeopod ungulate was not recognized in their system, and the underlying principle of Cope's system, since adopted by Marsh, and many of the younger school of palæontologists, rests upon a secure basis of fact. The real problem is, therefore, to ex-

[*] Ueber einige Beziehungen z. d. Säugethierstämmen alter u. neuer Welt. Zurich, 1888.

clude the variable elements, and ascertain those which are constant in the ordinal divisions; of course, no sharp lines of division, such as were apparent to the older naturalists, exist as we descend in the mammalian series.

First: We observe that while the metapodials play an important part in the displacement, the separate metapodial articulations are not available for taxonomic purposes in the larger divisions above the Protungulata. In the carpus there are practically but two types of articulation, the "serial" in the absolutely primitive and in some later forms, and the "alternating" in all but the highly specialized "adaptively reduced" Artiodactyla. There are no stages which are of more than family value.* In the tarsus the primitive serial type is retained almost unmodified in the Proboscidia and Hyracoidea, and in the early equine and Hyrachyus series it passes into the "plane serial," and into the alternating in the Palæosyops series.† The remaining Diplarthra show great variation in the mode of metatarsal articulation, so that there is no single type characteristic of all the genera of the *Tapiridæ* or *Rhinocerotidæ*; *Aphelops, Aceratherium, Atelodus* and *Rhinoceros*, each has a different type of metatarsal articulation.

Second: In the tarsus Prof. Cope's definitions and principles will not strictly apply, first, because the astragalus extends over the cuboid in some of the earliest and not in some of the more recent Mammalia, and this displacement is thus by no means distinctive as between the lower and higher types. The astragalus extends upon the cuboid in one or more members of the "taxeopod" Hyracoidea (*Dendrohyrax*) and Condylarthra (*Periptychus*), and in all the Amblypoda, to a much greater extent than in many of the diplarthrous Perissodactyla (see the Equus, Hyrachyus, Paloplotherium series, p. 548).

As Rütimeyer points out, there is no parallelism between the diplarthrism of the fore and hind feet—diplarthry may be rapidly developed in one while taxeopody persists in the other. This arises from the fact that the mechanical problems of adaptation to the unguligrade position are dissimilar in the fore and hind feet owing to the difference both in the arrangement of the bones and in the motions. Among the Hyracoidea, *Hyrax* is a taxeopod in both feet, while *Dendrohyrax* has a taxeopod manus and diplarthrous pes. In the Proboscidia the manus is nearly serial, sometimes completely so, while the pes is invariably diplarthrous, although well distinguished

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* Kowalevsky's "adaptive reduction" arises independently in the Bunodonta and Selenodonta.

† There are some other marked illustrations of the variable nature of the podial articulations. The confluence of one or the other of the three astragalo-calcaneal facets is subject to specific variations; compare *R. incisivus* and *R. leptorhinus* (De Blainville, Osteogr.). Compare the astragalo-cuboidal facets in *Tapiris americanus* and *T. indicus*. The lunar-magnum facet differs widely in *Equus burchelii*, *caballus* and *asinus*.

by the movement of the navicular above the cuboid. Cope has himself recognized the difficulty arising in the Amblypoda from the union of limited diplarthrism in the carpus with extreme diplarthrism in the tarsus. In *Macrauchenia* we find a peculiar displacement in the carpus and no astragalo-cuboidal contact in the tarsus.

The fibulo-calcaneal facet may be regarded as a secondary character, since it is developed independently in so many phyla—as a trochlear joint in *Meniscotherium*, *Macrauchenia*, the Artiodactyla; as a supporting facet in the Proboscidia, Titanotheridæ and Hyracotheridæ. It cannot be employed in ordinal classification (*vs.* Cope, Tert. Vert., p. 378).

Third: The definitions based upon the carpal series cannot be availed of strictly as employed by Cope.* For (1) in some of the Amblypoda (*Uintatherium*) the scaphoid has a broad posterior facet upon the magnum, although of less extent than the lunar unciform facet. (2) In the Proboscidia the lunar frequently rests upon the trapezoid, and sometimes upon both the trapezoid and unciform. (3) In Macrauchenia the lunar is entirely excluded from the unciform, the cuneiform resting upon the magnum.

A comparison of the entire evolution of the carpus and of the tarsus shows that the former, while more complex, is subject to more definite laws, and is therefore more available for purposes of classification. The carpal characters are constant and distinctive, but not exactly as interpreted by Prof. Cope†—we must look at the manus as a whole, including the metacarpals. The tarsal displacements can be employed for subsidiary definition only. It has thus been shown that Cope's whole system breaks down if we attempt to establish a parallel between the evolution of the carpus and the tarsus in relation to displacement.

With these limitations the principle of classification of the ungulates by foot structure loses the universal application claimed for it by Cope, but is by no means invalidated to the extent held by Rütimeyer.‡ Giving the first rank to the characters of the manus, and second to those of the pes, the following modifi-

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* Tertiary Vertebrata, p. 376.

† Tertiary Vertebrata, p. 377. "In the first place I find the diversity in the structure of the carpus to be greater in the relations of the magnum and scaphoides than in the relations between the unciform and the lunar. In other words the trapezoides and magnum are more variable in their proportions than is the cuneiform. * * * I therefore view the relations of these bones as more characteristic." In the succeeding section, V, this view is shown to be untenable.

‡ *Op cit.,* p. 18.

cation of Cope's table is proposed; several subordinal characters being omitted for brevity :

A.—a. Carpals serial.
  I. TAXEOPODA.
  1. Primitive. Protungulata.
      c. Plantigrade.
      e. Tarsals serial.
      b. Metapodials serial.
  2. Intermediate. Condylarthra.
      c. Subdigitigrade.
      e. Tarsals serial.
      b. Metapodials displaced.
  3. Recent. Hyracoidea.
      c. Plantigrade.
      e. Tarsals serial or displaced.
      b. Metapodials displaced.

B.—a. Displacement of first upon second row of carpals not uniform.
      b. Metapodials displaced.
  II. AMBLYPODA.
      c. Semi-plantigrade, plantigrade.
      d. Lunar upon cuneiform.
      e. Astragalus upon cuboid.
  III. PROBOSCIDIA.
      c. Semi-plantigrade.
      d. Carpals serial, or lunar upon trapezoid.
      e. Astragalus and navicular upon cuboid.
  IV. (MACRAUCHENIA.)
      c. Digitigrade.
      d. Scaphoid and unciform upon magnum.
      e. Tarsals serial.

C.—a. Displacement of first upon second row of carpals uniform.*
      b. Metapodials displaced.
      c. Digitigrade to unguligrade.
      e. Tarsals more or less displaced.
  V. DIPLARTHRA.
  1. Perissodactyla.
      f. Mesaxonic.
      c. Carpal displacement extreme in reduced forms.
      e. Astragalo-cuboidal facet flat.
  2. Artiodactyla.
      f. Paraxonic.
      a. Carpal displacement limited in reduced forms.
      e. Astragalo-cuboidal facet ginglymoid.

The position of the Toxodontia and of *Macrauchenia* is doubtful.

The three subdivisions above employed (A, B, C) bring out what appears to be a fundamental distinction between Orders II, III, IV and V. The significance of the diverse carpal displacement in the Artiodactyla and Perissodactyla is shown in the next section.

V. THE PRINCIPLES OF DISPLACEMENT.

The evolution of the manus and pes of the ungulates included the following processes: (1) Elevation from the plantigrade to the digitigrade position; (2) growth of certain elements and reduction of others, including the loss of lateral parts; (3) displacement of the elements of the podium and metapodium from the primitive serial arrangement; (4) coalescence of parts primitively distinct. All these processes interacted upon each other, and so far as they can be distinguished, took place, for the most part, in the order named. That is, elevation usually preceded the metatrophic or unequal growth of parts and the elongation or vertical growth of the metapodial elements involved the mutual displacement or interlocking of the podials and metapodials. The effects of these processes were in the nature of adaptations correlated with changes in the entire body which were induced by the habitat, manner of feeding, character of the ground, necessity of speed both in ranging for

*See this Memoir, p. 541. The scapho-magnum = lunar-cuneiform facet.

food and escaping enemies. Kowalevsky* and Rütimeyer† have treated these factors very fully. Then there were the changes in the movement of the limbs with reference to the axis of the body ; for example, in the evolution of the horses Kowalevsky has directed attention to the atrophy of muscles which rotated the fore limb, resulting finally in a direct fore and aft motion. Another factor was the transmission of the weight unequally through the bones of the lower leg, as one or other of these elements grew or became reduced. Finally there were the influences which the reduction of the lateral digits in the artiodactyl and perissodactyl series exerted upon the central digits and upon the podial elements by modifying the principal lines of "impact and strain."

THE MANUS.

It has been shown that the modifications of the manus are more complex and yet proceed along more definite lines than those in the pes, and in spite of the great variety of influences exerted we can discover certain fixed laws of modification.

1. *Relations of growth, reduction and displacement.* As displacement changes the vertical relations of the three rows of podial elements to each other, it follows that there must be concomitant growth in some elements and reduction in others, otherwise some of the lateral parts would be left without support. That the displacement of an element, however, involves a principle distinct from mere growth and is an actual shifting or "rotation" process, although not to the degree maintained by Cope,‡ is shown by a number of facts. First, as to the chief factors in each process. Growth is more directly brought about by vertical pressure, as seen in the magnum of the Equidæ ; and displacement, by lateral strain, as seen in the shifting of the metapodials to the ectal side of the carpus. Displacement is apparently arrested in such a series as *Hyracotherium*, where the fore limb acquired an orthal movement and, the entire vertical pressure passing through the median toe, the growth of the magnum counteracted the incipient displacement of the lunar upon the unciform. We cannot explain the lateral facets of metacarpals II and III in the pentadactyl Amblypoda and Proboscidia as due merely to growth of the elements displaced, for the digits are strikingly equal in size ; they both extend to the ectal side, and what mc. III gains upon the unciform it apparently surrenders to mc. II upon the magnum. Finally, there is every reason to agree with Kowalevsky that the reduc-

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* Monogr. der G. Anthracotherium, Palæontographica, Bd. XXII, 1873, pp. 161-5.

† *Op. cit.*, pp. 17-24.

‡ The Perissodactyla. American Naturalist, 1887, p. 986.

tion of the lateral digits in the ungulate foot is largely the direct result of elevation to the unguligrade position which rendered useless the shorter lateral digits of the plantigrade foot. Yet every step in reduction of the toes influenced the growth and displacement of the more proximal elements.

It can be demonstrated that these three processes were concomitant, and while resulting directly or indirectly from the same causes, were not affected in the same degree by them. The problem may be expressed in this way: What were the principal factors in each of the above processes, and how did these processes interact.

2. *Theories of modification.* As Kowalevsky was unaware of the primitive serial arrangement of the podial elements, his studies were chiefly directed to the phenomena of growth in the metapodials and the manner in which in the adaptive and inadaptive artiodactyls and in the perissodactyls the second and third metacarpals spread from their respective carpals to the adjacent elements.[*]

Ryder[†] later pointed out the effect of impacts and strains upon the phenomena of reduction of the digits.

Cope,[‡] the first to recognize the common development of the ungulate foot from a primitive serial type, was also the first to advance a " displacement " theory: " As the foot is descending towards the ground it is with the distal part of the leg rotated from within outwards. The rotation of the foot is promptly arrested at the moment of its contact with the ground, and the effect of this arrest is to produce a torsion of the leg, and a pressure from within outwards of the proximal or moving element of each articulation against the distal or fixed element."

An adequate theory for the displacement phenomena must, however, explain the shifting of the metacarpals and metatarsals, as well as that which takes place between the two rows of carpals and tarsals. The latter always takes place (excepting in the Proboscidia) in the same direction. Prof. Cope's theory has therefore to meet the apparently fatal objection that the arrest of rotation to the ectal side would be first felt at the junction of the metapodials and podials, and if it were of the character he describes, would continually tend to separate these joints and displace them to the ental side, whereas we find them provided with facets to resist pressure towards the ectal side.

It is a significant fact, recently pointed out by Weithofer,[§] that in all ungulates in which the radius is larger than the ulna, the proximal row of carpals is displaced

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[*] Monog. der Gatt. Anthracotherium, 1873, p. 142.

[†] On the Laws of Digital Reduction. American Naturalist, 1877, p. 603.

[‡] The Perissodactyla. American Naturalist, 1887, p. 986.

[§] Einige Bemerkungen über den Carpus der Proboscidier. K. Ant. Weithofer, Morph. Jahrb., 1888, p. 508.

to the ectal or ulnar side of the distal row; in the one order (Proboscidia) in which the ulna is the larger bone, the proximal row is moved, if at all, to the ental or radial side.

3. *Relation of the size of the radius and ulna to displacement.* It thus appears probable that the transmission of the main body weight through the ectal or ental side has caused displacement between the first and second row of podial elements respectively to the ental or ectal side. But this is clearly not the only factor; if it were, this displacement should be proportional in the Diplarthra to the enlargement of the tibia and radius respectively; this is certainly not the case either in the carpus or tarsus.

In the early horse series (*Hyracotherium*), in which the radius is enlarged and the ulna reduced more rapidly than in any other, the ectal displacement of the lunar is not so uniform nor so rapid as in the *Rhinoceros* series in which these bones retain approximately their primitive proportions. Compare the *Triplopus* carpus, with the scaphoid resting chiefly upon the magnum and the lunar resting wholly upon the unciform, anteriorly, as a type of extreme displacement, with that of *Hyracotherium* or *Epihippus*, in which the displacement is slight. The latter presents much less divergence from the taxeopod type, although the ulna is proportionately more reduced. We meet still greater difficulties in the pes, where, as seen by the contrasts in the members of the *Equus*, *Hyracodon* and *Rhinoceros* series, the extension of the astragalus upon the cuboid is seen to be entirely independent of tibial enlargement. Nor is this extension a resultant of weight, as proven by the diversity of the cuboastragalar articulation in *Dendrohyrax* and *Hyrax*. We reach the conclusion that while the direction of the displacement may be determined by the transmission of the main weight through the ental or ectal side, the degree of displacement is not proportionate to this enlargement, but is modified by other causes.

4. *Growth and reduction* take place by metatrophism, the separate elements of the foot being hypertrophied or atrophied by increased or diminished use, resulting in a transfer of nutrition, one element growing at the expense of another. We have to deal with the adaptations to both vertical pressure and lateral strain, since the motion of the limbs, of the fore limb especially, is not in a perfectly direct line. It may be assumed that the parts grow most rapidly which are subjected to the maximum resultant of these vertical and oblique forces. As a strong confirmation of the theory of displacement here advanced, it may be mentioned that from a study of the resistant facets the writer reached independently the same conclusions as to the motion of the fore feet as those drawn from the study of instantaneous photographs.

5. We are indebted to Prof. Harrison Allen's[*] studies of the celebrated Muy-bridge photographs for the following laws of quadrupedal motion : As the fore foot descends it passes under the body (p. 51), *i. e.*, inwards ; striking the ground, it arrests the torsion of the trunk as the shoulder is turning forwards towards the oppo-site side (p. 57) ; it strikes upon the outer border (p. 88) and leaves by the inner border (p. 50), so that the pressure of the body is borne from without inwards across the foot ; as the foot is raised the sole is everted (p. 50). It follows (*nobis*) that to strike upon the outer border the sole must be slightly inverted as the foot is lowered ; secondly, in so far as the trunk torsion is transmitted to the feet, the feet must be rotating upon their own axis from the outer to the inner side. Let us first see how this theory of foot motion agrees with the metapodial displacement.

6. The *metapodial displacement* is practically uniform throughout the Ungulata in the carpus, but very diverse in the tarsus. This difference is undoubtedly due to the fact that the fore foot is for support, the hind foot for propulsion. The latter moves forwards and backwards in a nearly straight line, thus the metapodials are variously displaced in accordance with slight lateral variations in this orthal move-ment. In the manus the second and third metacarpals invariably have ectal facets upon the magnum and unciform respectively. The only variation is in the adaptively reduced Artiodactyla in which the third metacarpal spreads also upon the trapezoid (Diag. 9). This disposition of the facets is perfectly adapted to resist the strain upon the metapodials as the foot swings inward in descent, this motion being univer-sal among the primitive types. Thus the ectal displacement of the metapodials be-gins with the elevation of the wrist joint and precedes the intercarpal displacement (see *Phenacodus*, Diag. 8). It does not advance but appears to be retarded by the elongation of the metapodials, as in the palæothere and equine line, as the lateral motion diminishes. The extension of these carpo-metacarpal facets is largely a matter of reciprocal growth, *i. e.*, the unciform, for example, extends inwards as the third meta-carpal extends outwards (compare Diags. 8, 9).

7. *Growth of the scaphoid and unciform.* As a result of metacarpal displace-ment and of digital reduction, the unciform, already supporting the fourth and fifth digits, received a portion of the third digit. As the fifth digit persisted longer than the first, both the motion of the foot striking upon the outer border and the trans-mission of the direct weight through three digits contributed the maximum vertical and lateral strain to the ectal side of the second row of carpals and especially to the unciform, while in the bones of the first row the ental side, the scaphoid and lunar,

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[*] The Muybridge Work at the University of Pennsylvania. Materials for a Memoir upon Animal Locomotion. By Harrison Allen, Phila., 1888.

received the maximum pressure and lateral strain. At the same time, the ectal or ulnar side of the upper row and ental or radial side of the second row received a diminished pressure and strain by the reduction of the ulna and loss of the first digit respectively.* At all events the scaphoid grew outwards and the unciform grew inwards in all the Diplarthra; they thrust the lunar and magnum apart over the unciform and beneath the scaphoid respectively, in many cases without any actual or relative increase in the size of these elements, as demonstrated by the extremely small size of both the magnum and lunar in the greatly displaced carpus of *Triplopus* or *Hyracodon.* Thus what appears to be a *rotation* of the bones of the upper
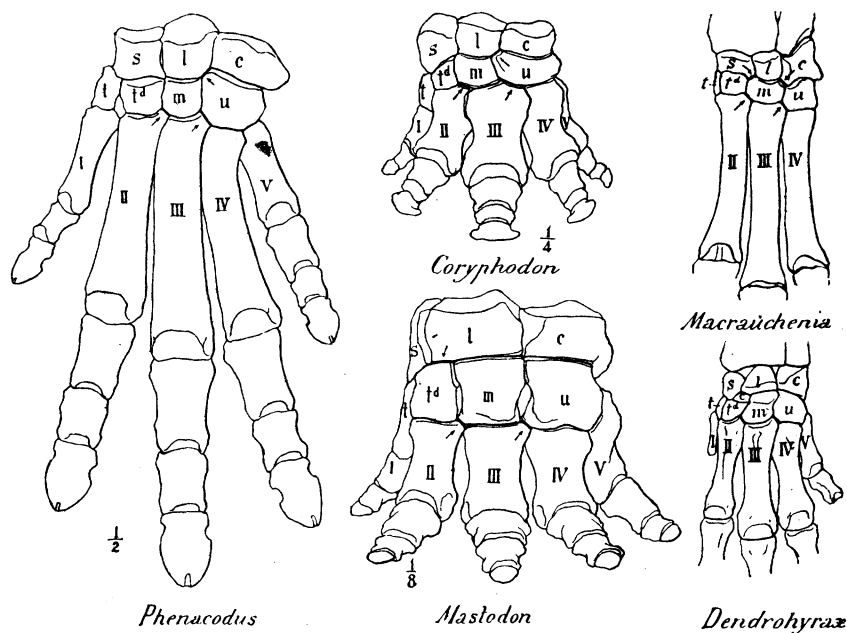
Coryphodon

Macrauchenia

Phenacodus   *Mastodon*   *Dendrohyrax*

DIAG. 8.—The displacement of the bones of the manus in the Ungulata, I. *Phenacodus primævus*, from original in the Cope collection. *Coryphodon hamatus*, after Marsh. *Dendrohyrax arboreus*, from original in the Princeton collection. *Macrauchenia patachonica*, after Gervais. *Mastodon Americanus* from original in Princeton collection. The oblique arrows indicate the direction of displacement.

row upon the second row, is in reality the growth of the scaphoid and unciform towards the median axis of the foot. This is carried to its extreme in the tridactyl Perissodactyla, in which the mesial borders of the unciform and scaphoid are almost in contact in the mesaxial line, i. e., in the line carried through the middle toe.

This explanation is still inadequate, because we find, first, that under certain conditions the lunar shows a marked tendency to expand, and secondly, the mesial growth of the scaphoid and unciform ceases.

* A convenient illustration of the effect of digital reduction upon the carpals was remarked by Dr. Scott in the reduction of the scaphoid in the inadaptively reduced Artiodactyla—the scaphoid resting upon the trapezoid and the trapezium supporting the functionless second digit only.

8. *Reduction and displacement.* There is unquestionably an intimate connection between the reduction of the lateral toes and displacement. Ryder* has pointed out that where the strains are equally distributed among all the digits, there is rarely any specialization of toes, and that in general the reduction of the digits is in direct ratio to the increase of mechanical strains and the frequency and severity of impacts.

Cope† has recently assigned displacement as a cause or as preceding digital reduction. This supposition is rendered improbable by the numerous instances of reduction without displacement, for instance, the first digit of the manus and first and fifth digits of the pes in *Hyrax;* secondly, by the numerous cases of extreme reduction, as in the *Pecora,* with limited displacement.

Now if we consider the manus with reference to the correlation of certain types of reduction and displacement, without reference to phylogeny, we find six types:

I. The first type is theoretical, and will be found among the Puerco Condylarthra. In it there is no reduction or displacement.‡ *Phenacodus* is the nearest known representative, in which, however, there is initial reduction, metapodial displacement, slight intercarpal displacement, and a marked tendency to the mesaxonic type. II. The second type embraces the Amblypoda, with the lunar strongly and the scaphoid slightly or not at all displaced. There is no distinct median axis. III. The third or proboscidian type differs from the last only in the direction of the lunar displacement, which is usually upon the trapezoid. The median axis is not well defined. IV. The fourth type is shown in a typical condition in *Titanotherium,* also more or less marked in all tetradactyl Perissodactyla, as well as in all tetradactyl and didactyl Artiodactyla; it represents a stage in which the perissodactyl foot approaches the artiodactyl, the third and fourth toes spreading upon either side of the mesaxial line; the displacement of the carpals is apparently arrested, the lunar retaining some foothold upon the magnum. All tridactyl and monodactyl ungulates pass through this stage. V. The fifth type is invariably associated with tridactylism, incipient (*Hyrachyus*) or advanced (*Aphelops*), in which displacement is carried to an extreme and the mesaxial line passes directly through the third digit. VI. The sixth is associated with monodactylism and entire loss of lateral motion, in which the primitive displacement is counteracted by the growth of the magnum. VII. The seventh is represented in *Macrauchenia,* the lunar showing extreme reduction, both the scaphoid and unciform articulating with the magnum.

* On the Laws of Digital Reduction. American Naturalist, 1877, p. 603.

† "This rotation has resulted, sooner or later, in the loss of the first digit." American Naturalist, 1889, p. 986.

‡ The pes of *Periptychus* is so closely similar to that of the bear, the manus may be assumed to be of the same type.
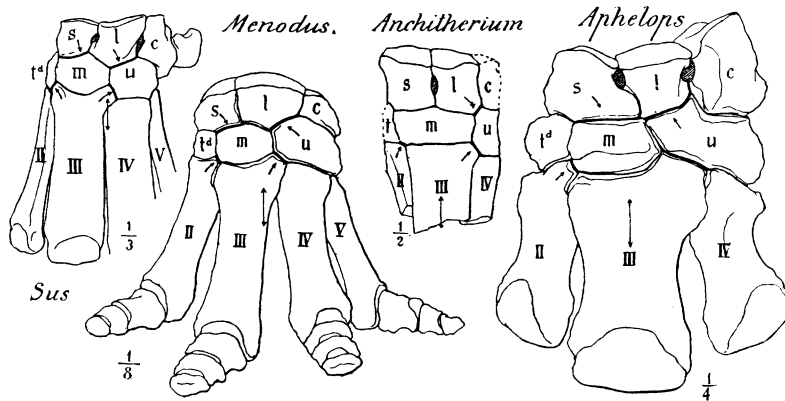
First. In Types II and III the unreduced, nearly isodactyl and semiplanti-grade forms, the *Amblypoda* and *Proboscidia*, the unspecialized spreading toes trans-mit the strain from every side. We observe a marked increase in the size of the lunar. Among the Proboscidia the lunar either rests upon the magnum only or upon the magnum and trapezoid; this is the common condition; or upon the magnum, trapezoid and unciform (see page 539).

Second. In all the genera of the reduced types, excepting the highly spe-cialized Types VI and VII, it is a remarkable fact that the scapho-magnum and lunar unciform facets are subequal. It appears from a comparison of the vast num-ber of forms included in Types IV–VI, that reduction, altering as it does the entire system of digital strains, has had some definite influence in limiting or widening the extent of these facets, and that Prof. Cope has put the effect before the cause in stating that displacement precedes reduction. Schlosser has rightly reversed this relation.*

The permanent tetradactyl condition in the perissodactyls of Type IV, like the artiodactyl didactylism is paraxonic, *i. e.*, the greatest vertical strain is not trans-mitted directly through the median toe but between the third and fourth toes, this, with the lateral strain coming from the functional fifth toe, in some manner limits the growth of the scaphoid and unciform, and in many instances results in the spreading of the lunar in both directions; it will be observed that in nearly every case the lunar is directly in the mesaxonic line. Where the four toes spread, as in *Titano-therium*, the metapodial strains must be somewhat analogous to those in the Probos-cidia and Amblypoda—at all events the growth of the lunar in each instance suggests such an analogy.

As this condition of the lunar occurs in widely separated phyla and in a large

Op. cit., p. 113 : "Gleichzeitig mit dieser Reduktion der Seitenzehen findet auch eine Aenderung in der Anord-nung der Carpalien und Tarsalien statt."

number of forms, it cannot be due to mere coincidence, but must be the result of certain modifications of the pressure and strain transmitted to the carpus in paraxonic types. The loss of the lateral toes in the highly reduced Artiodactyla, in which the pressure is most perfectly divided between mts. iii and iv, from Eocene to recent times, has not been accompanied by any alterations of the relations of the lunar to the magnum and unciform (see Anoplotherium and Cervus), apparently because there is no alteration in the axis of the metapodium. But in the Perissodactyla the reduction of mc. v, as can be readily observed in the rhinoceroses (see De Blainville, Osteographie, *R. tetradactylus* of Auvergne, of Sansans, and *R. sumatrensis, unicornis, bicornis*), is accompanied step by step by the displacement of the lunar from the magnum. Lateral compression of the carpus has nothing to do with this displacement, because the tapir, which is even now in the transition stage between Types IV and V, has a much narrower carpus than *Aphelops*. The tapir manus is now in the stage of evolution which was passed by the rhinoceros in the Miocene period.

It follows from these cases that reduction *per se* does not influence displacement, but only in so far as (in the Perissodactyla) by releasing the carpus from the pressure of the v digit it brings the major axis directly through the centre of the third digit, as seen in Type V. This type thus embraces a large number of forms, in which reduction of the fifth digit has been very rapid. The writer can find no exceptions to the law that mesaxonic tridactyl types of all the Tertiary periods show the extreme of diplarthrism. *

Dr. Scott has called the writer's attention to a third correlation of the lunar and reduction, as found by a comparison of the lunar, scaphoid and unciform in the adaptive and inadaptive Artiodactyla. In the inadaptive types (Enteledon, Anoplotherium, etc., see Kowalevsky) the lunar is enlarged at the expense of the scaphoid; the latter resting upon the trapezoid, which in turn supports only the rudimentary second digit, the third digit forming no trapezoidal union. In the adaptive types, on the other hand, the third digit acquiring a trapezoidal facet, the scaphoid is somewhat larger and the lunar less enlarged.

Tarsus.

The above observations apply chiefly to the carpus, but precisely the same principles operate in the tarsal displacements.

*The manus of *Palæotherium medium*, as figured by Kowalevsky (Palæontographica, Bd. XXII, Taf. VII), presents an exception. But reference to De Blainville's figure and to a cast of the original foot recently presented to Princeton by the Paris Museum, shows that Kowalevsky's figure is incorrect. There is no extensive lunar magnum facet, such as he represents.

The rapid reduction of the fibula accompanying the orthal movement of the limb hastens the displacement of the astragalus, in advance of any displacement in the carpus.

The growth of the astragalus upon the cuboid and the cuboid beneath the astragalus are reciprocal. The former may be compared to the scaphoid and lunar displacement, the latter to the growth of the unciform beneath the lunar, *i. e.*, towards the mesaxial line.

The line of association of reduction with certain forms of displacement observed in the manus has a parallel in the astragalo-cuboidal displacement. It will be observed that in the artiodactyl or paraxonic types there was a primitive disposition to form an astragalo-cuboidal facet, adapting the middle axis of the astragalus and calcaneum to the middle axis of the metapodium, which here passes between the second and third digits. On the other hand the *Hyracotherium, Paloplotherium* and *Hyracodon* mesaxonic types, as they all tend to monodactylism, show an arrest of displacement, owing to the growth of the third digit producing conditions similar to those in the monodactyl carpus; while genera of the iso-tridactyl mesaxonic type, the tapir, rhinoceros, etc., all show extreme astragalo-cuboidal displacement exactly parallel to that in the carpus.

CONCLUSIONS.

The laws of adaptation of the serial plantigrade foot to digitigradism may be summarized as follows :

1. Displacement is effected by the growth, arrested growth, or reduction of different elements, and takes place in the direction of the greatest lateral strain, being most rapid in the elements which are subjected to the maximum vertical impact and lateral strain.

2. The direction and degree of intercarpal displacements are adapted to the gradual alteration of the major axes in the bones of the fore arm and of the metapodium respectively, as brought about by reduction, and tend to maintain these proximal and distal axes in the same vertical line.

3. The initial displacement, however, preceding and independent of reduction, is the ectal movement of the metapodials, adapting these elements to resist the strain of the "stroke" upon the outer border, as the foot extends downwards and inwards.

4. In the unreduced isodactyl types, the strain of the spreading metapodials

converges to the centre of the carpus, without a defined median digital axis, and the lunar spreads to the ectal or ental side according as the respective growth of the radius or ulna alters the major axis of the fore arm.

5. In the Diplarthra the major axis of the fore arm passes through the radius, and through the third digit (M e s a x o n i a) or between the second and third digits (P a r a x o n i a). The outward displacement of the entire upper upon the lower row of carpals is apparent, not real; the magnum and lunar are arrested in growth, and the lunar remains almost directly in the mesaxial line; what actually takes place is the ental growth of the unciform and ectal growth of the scaphoid towards the mesaxial line, thrusting the magnum and lunar apart.

6. This growth is affected by the reduction of the lateral digits in so far as this alters their relation to the major axis of the metapodium. Where reduction leaves the major axis between the third and fourth digits, this growth is arrested; where it leaves it directly through the third digit it is extreme; where the third digit alone transmits the main impact, the displacement is neutralized by the growth of the elements which directly support this digit (i. e., magnum and cuneiform 3).

EXPLANATION OF PLATES.

Plate VII.

PROTOREODON PARVUS.

Fig. 1. S k u l l, side view ; 1*a*, base of skull and superior molars ; 1*b*, brain from above ; *ss*, sylvian g)rus ; *l*, lateral ; *m*, median gyrus.

2. I n f e r i o r   m o l a r s, internal view ; 2*a*, crown view.

3. Portion of c a r p u s with f i r s t   d i g i t.

4. H u m e r u s, anterior view of distal end.

5. T i b i a   a n d   f i b u l a, anterior view ; 5*a*, distal view.

6. P e s, anterior view, of a larger individual.

7. P h a l a n g e s, of fourth digit.

8. M e t a t a r s a l   II, medial side of proximal end ; c_2, facet for mesocuneiform ; c_3, for entocuneiform.

LEPTOTRAGULUS PROAVUS.

9. L o w e r   j a w, side view, combined from specimens shown in Figs. 10 and 11.

10. L o w e r   j a w, inner view, showing pm. 4 and m. 1 ; *a*, crown view.

11. S e c o n d   a n d   t h i r d   l o w e r   m o l a r s of another specimen, inner view ; *a*, crown view.

12. U l n a   a n d   r a d i u s, proximal end.

13. S c a p u l a, distal end ; 13*a*, glenoid cavity.

14. M e t a c a r p a l   IV, anterior view ; 14*a*, proximal end ; *u*, facet for unciform.

15. Portion of t a r s u s, anterior view.

16. Cuboid.

(Figures natural size.)

Plate VIII.

DIPLACODON, see page 514.

Fig. 1–1*a*. F i f t h   c e r v i c a l   v e r t e b r a, anterior view, lateral view.

2. D o r s a l   v e r t e b r a, between *d*. 7 and *d*. 10.

3–4. L u m b a r   v e r t e b r a, lateral view, posterior view.

5. F e m u r, anterior view ; 5*a*, external view ; 5*b*, distal view.

6. T i b i a, anterior view ; 6*a*, distal view.

7. Left *os innominatum*, lateral view. $\times \frac{1}{5}$.

8. C a l c a n e u m   a n d   a s t r a g a l u s, front ; 8*a*, external ; 8*b*, posterior view of astragalus ; *c*, distal view.

9. C a r p a l s, proximal row ; probably belonging to a young individual ; *a*, proximal surfaces.   Reference to *Diplacodon* uncertain.

Plate IX.

DIPLACODON, see pages 515–16.

Fig. 10. U l n a   a n d   r a d i u s, external view ; 10*a*, distal view ; 10*b*, anterior view ; 10*c*, internal view.

11. H u m e r u s, posterior view ; 11*a*, external view.

12. L e f t   s c a p u l a, outer surface, $\times \frac{1}{5}$; *a*, glenoid fossa.

13. R i g h t   m a n u s, $\times$ 1 ; the carpals are restored from *Palæosyops* and *Titanotherium ;* the metacarpals are slightly foreshortened ; *b*, mcs. II–IV, proximal view ; *a*, mc. IV, distal view, $\times \frac{2}{3}$.

14. S u p e r i o r   m o l a r, probably m^2.

15. A x i s, belonging to a smaller individual ; side view.

Plate X.

ISECTOLOPHUS ANNECTENS, see page 520.

Fig. 1. S u p e r i o r molars of left side ; 1*a*, external view of same.

2. I n f e r i o r m o l a r s, crown view ; 2*a*, external view of m_3.

11. I n f e r i o r s e r i e s of a younger individual (No. 10,399).

3. L e f t c a r p u s, front view, with the metacarpals partly restored.

4. R i g h t c u b o i d, external view ; 4*a*, anterior view ; 4*b*, superior view, showing *ac* (astragalar) and *cc* (calcaneal) facets.

5. P h a l a n g e s probably belonging to the second and third digits.

6. M e t a t a r s a l s, distal portion, probably of III and IV ; *a*, distal faces of same.

7. T i b i a, distal face.

8. Proximal view of radius and ulna.

AMYNODON INTERMEDIUS, see page 508.

10. P a l a t e a n d s u p e r i o r d e n t i t i o n ; 10*a*, side view of superior dentition.

MESONYX UINTENSIS.

9. I n f e r i o r p r e m o l a r - m o l a r s e r i e s, internal view.

Plate XI.
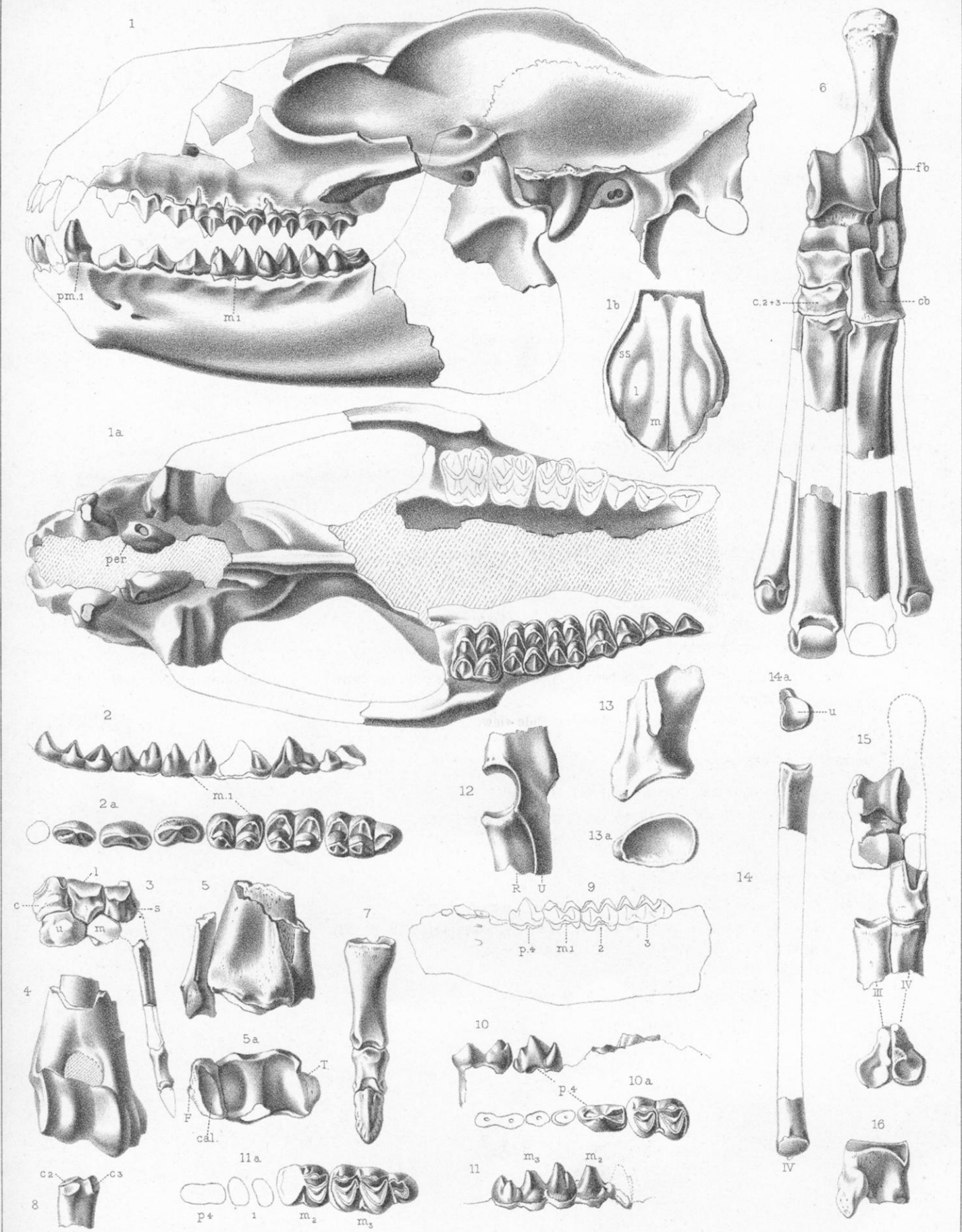
PLESIARCTOMYS SCIUROIDES.

Fig. 1. S k u l l, from above ; 1*a*, base of skull ; 1*b*, side of skull ; 1*c*, crowns of superior molars ; 1*d*, crowns of inferior molars and incisor.

2. T i b i a, side view ; 2*a*, h u m e r u s, side view.

EPIHIPPUS UINTENSIS, see page 529.

3. L o w e r j a w, from above ; 3*a*, side view.

4. F o r e a r m a n d m a n u s, front view ; 4*a*, side view.

5. T a r s u s, front view.

TRIPLOPUS OBLIQUIDENS, see page 525.

6. S u p e r i o r m o l a r s, crown view ; 6*a*, external view.

7. I n f e r i o r m o l a r s and alveoli, type of *T. obliquidens* (No. 10,402).

8. M a n u s, front view.

9. P e s, front view.

10. Third s u p e r i o r m o l a r (No. 10,402).

PROTOREODON, 1–8.   LEPTOTRAGULUS, 9–16.

DIPLACODON, 1-8.

DIPLACODON.

ISECTOLOPHUS, 1-8. AMYNODON, 10-10a. MESONYX, 9.

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PLESIARCTOMYS, 1–2a. EPIHIPPUS, 3–5. TRIPLOPUS, 6–10.